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Cranial Skeletons of *Hipparion* (Perissodactyla, Mammalia) from Maragheh (Turolian, Late Miocene), Northwest Iran

By

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Abstract

Cranial skeletons of *Hipparion* collected from Maragheh, northwest Iran were studied. On the basis of facial and dental morphology, four morphotypes of skull were recognized in Maragheh hipparions, namely, 1) *H. gettyi*; 2) *H. moldavicum*; 3) *H. prostylum*; and 4) *H. urmiense*. The morphotypes in the cranial elements were correlated with those in the postcranial bones. By this the correspondence between the facial morphology and postcranial proportions are attained, allowing increase of characters available for studies on functional morphology and taxonomy. Based on those characters, we discussed phylogenetic relationships of the Maragheh *Hipparion* with other Eurasian late Miocene hipparions. They show similarity to those from the Turolian beds in northern China. **Key words:** *Hipparion*, Perissodactyla, Maragheh, Turolian, Cranial, late Miocene, Iran, taxonomy, phylogeny.

1. Introduction

The taxonomic characters of the hipparion skull lie in the upper dentition and the facial morphology as well as size and proportions of the snout. Since among the fossils the lower jaw is often isolated from the corresponding upper jaw, its use for taxonomy is limited to higher taxonomic levels (e.g., hipparionid and caballoid type of the double knot). The Maragheh hipparions were classified on the basis of cranial characters and a correlation with postcranial morphotypes was carried out. The postcranial skeletons from Maragheh were examined and classified by WATABE and NAKAYA (this volume).

2. Method and Materials

In order to compare the relative location of the POF to the orbit, we used POB/P2-Orbit scatter diagram as suggested by FORSTÉN (1983). Those two variables were transformed to a logarithmic scale and plotted to represent the difference in proportion.

The size of the cheek teeth is represented by transverse width of the M1, and anterior

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and posterior width of the m1. The first permanent molars (M1 and m1) are used in scatter diagrams, because they are most frequently preserved and sufficiently worn in most specimens available.

The canine length to width scatter diagram was made to define sex of the specimens.

The values of measurements on the muzzle region were transformed to a logarithmic scale and plotted on a width-length scatter diagram for comparison of snout proportions. In our comparison, the muzzle width is represented by two measurements: the distance across the posterior edges of canines in the alveolus; and the distance across the posterior edges of third incisors. The snout length is also represented by the distance between the P2 and I3 (diastemata length); and by the distance between the prosthion and the mid point between the anterior edges of left and right P2.

For simultaneous comparison of the shape and location of the POF, ratio diagrams on facial measurements are used. By use of the ratio diagram the comparison of POF indices proposed by GROMOVA (1952) are possible.

The materials of the Maragheh hipparions were examined in the collections of the following places Museum National d'Histoire Naturelle, Paris; Naturhistorisches Museum, Vienna; and Kyoto University, Department of Geologiy and Mineralogy. For comparison of the Maragheh hipparions, Vallesian and Turolian hipparions from Eurasia were also examined. These data include those collected by us, and published and unpublished ones with permission.

Abbreviations

POF: Preorbital fossa.

POB: Preorbital bar, the space between the posterior rim of POF and anterior rim of the orbit, and its width.

IOF: Infraorbital foramen.

FC: Distance between the ventral rim of POF and the facial crest.

APL: Antero-posterior length of the occlusal surface of teeth.

TRNW: Transverse width of the occlusal surface of teeth.

PRTL: Protocone length including enamel.

PRTW: Protocone width including enamel.

D/d: upper/lower deciduous teeth.

I/i: upper/lower incisor.

C/c: upper/lower canine.

P/p: upper/lower premolar, P4 is upper fourth premolar.

M/m: upper/lower molar, m2 is lower second molar.

P3-4, p3-4, M1-2, m1-2: collective term for indistinguishable isolated teeth (e.g. P3-4 refers to upper third and fourth premolars).

BMNH: British Museum of Natural History, London.

KNHM: Naturhistorische Museum, Wien. The specimens' numbers begin width "A" or "W" mean they belong to KNHM.
KUAC: Department of Geology and Mineralogy, Kyoto University.
MMTT: National Muséum of Natural History, Tehran, Iran.
MNHN: Museum National d'Histoire Naturelle, Paris.
MAR: Maragheh specimens of MNHN.
MG: Musei Gruzii, Tbilisi.
All measurements in millimeters.

Anatomical terms used in this paper are based on GETTY (1975) and EISENMANN et al. (1988).

3. Taxonomic Value of Cranial Characters

Dental Morphology

Dental morphology has been employed as a taxonomic criterion in hipparion taxonomy by many authors. Such dental characters are as follows: degree of the enamel plication, number of pli caballin, relative size and shape of protocone, occlusal relief, development of stylar elements, and hypsodonty.

Many new species have been erected on the basis of dental characters, even of a single character. However, these characters are variable in single dental locus of single individual and are affected by differences in the degree of wear. For example, severely worn teeth show simple enamel plications and a rounded protocone. On the other hand, little worn teeth exhibit a higher relief of the occlusal surface than strongly worn teeth, and the anterior teeth (premolars) have a lower relief than the posterior teeth (molars) in a single tooth battery.

The characters of the upper cheek teeth can be used as valid taxonomic criteria if the wear stage of each specimen is identified, and the specimens are compared for similar wear stages (age). The plication count of the enamel plication and the protocone shape have taxonomic value in adult specimens with medium worn teeth.

It is very difficult to detect taxonomic characters useful for a species level in the lower cheek teeth. The stylids, such as the protostylid and ectostylid, are variable in development. The ectostylid is often present in deciduous teeth, but not in the permanent ones (except in African Pleistocene forms). The development of the stylids are characters expressed by percentages for a single taxon.

The depth of the ectoflexid has been considered an useful taxonomic character despite its variation. In premolars the ectoflexids are shallow and in molars deep, mesiodistally (anteroposteriorly) dividing the isthmus into two parts. In strongly worn tooth rows, the ectoflexids may become deep even in P3 and P4.

The type of double knot (the outline of the metaconid and metastylid) is useful at

higher taxonomic levels than the species (GROMOVA, 1952). The hipparionid double knot is seen among Vallesian and early Turolian hipparions and the caballoid one among Ruscinian and Pleistocene forms, although exceptions exist (e.g. *Hipparion tchicoicum* of northern China with a hipparionid double knot: QIU et al., 1987). In early wear stages, the metaconid and metastylid show irregular and angular outline.

POF Size and Its Location as Taxonomic Characters

There are two main ideas regarding the taxonomic value of the POF: 1) taxonomic value at species level (GROMOVA, 1952; FORSTÉN, 1983), 2) taxonomic value at supraspecific level (SKINNER and MACFADDEN, 1977; WOODBURNE and BERNOR, 1980; and others). Although it has been maintained that the POF is sexually dimorphic or individually highly variable (OSBORN, 1918; PIRLOT, 1953), these interpretations do not correspond with the results of the observations by many authors (WOODBURNE and BERNOR, 1980; FORSTÉN, 1983 and MACFADDEN, 1984; and others).

The POR morphology is taxonomically useful but it is affected by the animal's overall size. Generally, larger animals have larger POF size and POB length (distance between POF and the orbit), when they have the POF. There is also a possibility that allometric relationships exist between skull size and POF size and location.

WOODBURNE and BERNOR (1980) used orbital diameter as representing skull size. The skulls of hipparions are fragile and usually poorly preserved; it is very difficult to measure total skull size such as basal length (the prosthion to the basion), preorbital facial length (prosthion to anterior or posterior rim of the orbit), and even palate length (mid P2 anterior rims to anteriormost point of the choanae).

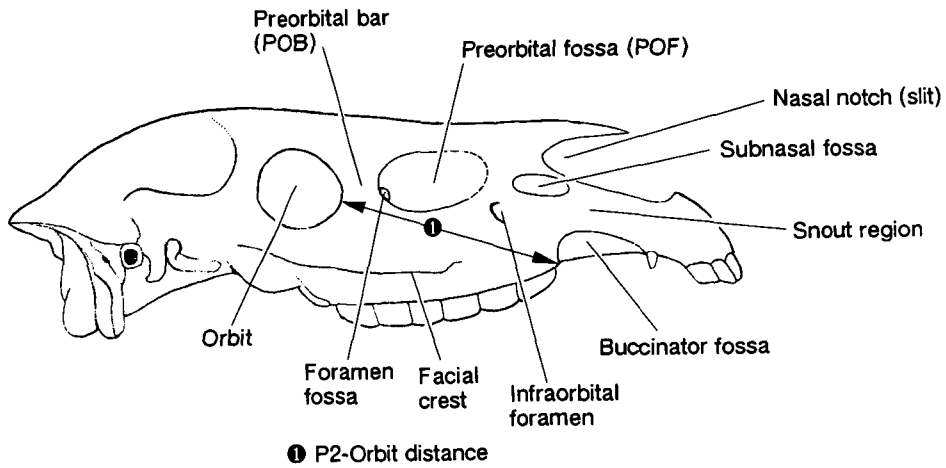

Fig. 1. Terminology of Facial region of *Hipparion*.

GROMOVA (1952) proposed P2-Orbit distance as a measure of skull size. It is seldom affected by crushing, nor by the lack of the fragile snout region or posterior cranial part. This is in practice a very suitable measurement as an indicator of skull size. This measurement was also employed by FORSTÉN (1980a, b; 1983) (Fig. 1).

POF Margins

The definition of the anterior rim of the POF has been utilized as a taxonomic character in *Hipparion* by several authors (WEBB, 1969; SKINNER and MACFADDEN, 1977; WOODBURNE and BERNOR, 1980; MACFADDEN, 1984). However, the definition of the peripheral margin of the POF is easily disturbed by skull deformation, such as dorsoventral crushing.

Generally the ventral rim is better defined than the dorsal one. Since the posterior rim often has a posterior pocket and a clear margin being easy to define, and POB length can be measured in most cases. Even in hipparions with the POF as only a shallow depression, e.g., *H. hippidiodus* from northern China, a well marked pit or posterior margin exists in a posterior part of the POF.

The definition of the anterior rim is highly variable compared to other rims of the POF. This is shown by observation of a single taxon from a single locality, such as *H. africanum* from Bou Hanifia (Algeria) and *H. prostylum* from Saloniki (Greece).

The value of the anteroposterior length of the POF, measured from the posterior to the anterior rim, is not stable since precise location of the anterior rim is very difficult to determine.

It is also often difficult to measure the dorsoventral height of the POF, because the dorsal rim is poorly expressed, and skulls are often compressed dorsoventrally.

The length of the POF can be well represented by the distance between the posterior rim of the POF and posterior rim of the IOF.

4. Sorting of Skull Specimens from Maragheh by Previous Authors

MECQUENEM (1908, 1911 and 1924–25) reported *Hipparion gracile* from Maragheh and compared the specimens with the Pikermi and Samos forms. He mentioned a less developed and more highly located POF of the Maragheh forms than of the Pikermi ones. He erroneously considered the morphological distinction between *H. mediterraneum* Hensel from Pikermi and *H. proboscideum* Studer from Samos as sexual dimorphism. The specimens MECQUENEM called "*H. gracile*" may belong to the hypodigms of *H. prostylum* from Maragheh.

By examining hipparion materials from the western Old World, WOODBURNE and BERNOR (1980) mentioned hipparionine forms from Maragheh. They divided the Eurasian hipparions into 4 supraspecific groups as: 1) Group 1, large hipparion of Vallesian

and Turolian age; 2) Group 2, Turolian hipparion with a triangular POF and a short POB; 3) Group 3, Turolian hipparion with a dorsally located shallow POF and a longer POB; 4) Group 4, Turolian hipparion of small-sized (dwarf form).

They included species from several localities into their groups and considered those groups phylogenetic entities at the supraspecific level. They recognized members of all four groups among the Maragheh hipparion materials. In addition, they distinguished two sub-forms in the materials of the Group 3, showing their successive phyletic relationship.

FORSTÉN (1983) studying the western Old World hipparion, including forms from the U.S.S.R. region which were lacking in WOODBURNE and BERNOR's work, concluded that the variation of facial morphology to be wide, and maintained that the western Old World late Micene hipparions could be included into a single genus *Hipparion* on the basis of the possession of a hipparionid double knot in the lower morrlars.

She distinguished two forms at Maragheh: 1) specimens assigned to Turolian hipparions with the POF placed close to the orbit; and 2) specimens assigned to Turolian hipparions with the POF placed for from the orbit. She did not give taxonomic names to her species of Eurasian *Hipparion*. The specimens of the first form have a facial morphology similar to that of *H. mediterraneum* from Pikermi. She suggested the possibility that the smaller variant of this form would be included into *H. matthewi*. The variation of the facial and dental characters of both forms partially overlaps. The specimens belonging to the second form are similar to *H. prostylum* from Saloniki and to *H. dietrichi-schlosseri* from Samos. The skull from the Kopran sub-locality was assigned to this form. Contary to this idea, WOODBURNE and BERNOR (1980) assigned the skull from Kopran sub-locality to their Group 1, large hipparions.

BERNOR (1985) summarized the Maragheh hipparions and presented the following taxonomic grouping: 1) *Hipparion gettyi* from the Kopran sub-locality; 2) *Hipparion* aff. *moldavicum*; 3) *H.* aff. *?matthewi*; 4) *H. prostylum*; 5) *H. campbelli*. Although he established two new taxa: *Hipparion gettyi* and *H. campbelli*, his classification of the Maragheh skulls is not essentially different from that of WOODBURNE and BERNOR (1980). *Hipparion gettyi* belongs to their Group 1 and *H.* aff. *moldavicum* to Group 2. *H. prostylum* and *H. campbelli* were assigned to Group 3. *H.* aff. *matthewi*, included into Group 4, is represented only by teeth and postcranials with small size. He presented a phylogenetic hypothesis of a successive evolutionary lineage from *H. gettyi* to *H. campbelli*, through *H. prostylum*. He considered that a reduction of the POF had occurred in this lineage. The relationships of the Kyoto collections of the Maragheh fauna and his stratigraphic data will be discussed in a later section.

All of the above mentioned three modern authors considered that the facial morphology (shape and location of POF) had taxonomic value, but there is variation to some extent. In other words, the facial morphology is a character which defines natural clades,

monophyletic groups. Determination of the position of those groups in the Linnean hierarchy: e.g. species, genus, etc., is a different problem, which is concerned with translation of the results of phylogenetic analysis to the system of Linnean hierarchy.

5. Proposals for Taxonomy of Maragheh Hipparions

1) *Hipparion gettyi*

POF location similar to that of the Turolian large hipparions from Samos and Pikermi, plesiomorphic POF morphology; deep posterior pocket; slender snout proportions; probably slender and long third metapodials, medium sized tarsal elements and phalanges.

2) *Hipparion moldavicum*

Short POB and FC, location of POF close to orbit and facial crest; well defined periphery of the POF (anterior rim ?); medially deep POF; sub-triangular shape of POF similar to that in *H. mediterraneum* from Pikermi; shallow posterior pocket; intermediate (subnasal) fossa not developed as in *H. mediterraneum*; nasal notch (slit) extracted at the level of P2; slender snout proportions; slender and long third metapodials, medium sized tarsal elements and phalanges. Small forms were identified by BERNOR (1985) as *Hipparion* cf. *matthewi*.

3) *Hipparion prostylum*

Moderately developed POF, located far from the orbit and dorsally shape of the POF oval; anterior rim of POF not well defined; shallow posterior pocket; robust snout proportions; robust(?) proportions and medium length of third metapodials, large sized tarsal elements and phalanges.

4) *Hipparion urmiense=H. campbelli* (BERNOR, 1985)

Shallow depression dorsally located on the facial region as POF; very slender snout proportions; slender proportions and medium length of third metapodials, large sized tarsal elements and phalanges (?).

6. Systematic Descriptions

Order PERISSODACTYLA OWEN, 1848

Superfamily EQUOIDEA HAY, 1902

Family EQUIDAE STEINMANN and DODERLEIN, 1890

Hipparion gettyi BERNOR, 1985

Synonymy:

Hipparion Group 1, WOODBURNE and BERNOR (1980)

"*Hipparion*" *gettyi*, BERNOR (1985)

Type: A skull, KNHM RLB 8401

Locality: Kopran sub-locality, Maragheh

Age: Turolian

Geographic range: Northwest Iran

Referred specimens from Maragheh: KNHM RLB 8401, (−150 m), adult-old female skull with snout region (L&RI1-I3, C) and L & RP2-M3, lacking brain case; KNHM W 8659, (−150 m/−115 m), adult palate with RP3-M3; KNHN W 86504, (−150 m/−115 m), very old maxillar bone with LP4-M3; KNHM W 86505, (−150 m/−115 m), very old maxillar bone with LP3-M3; KNHM W 8613, (−150 m/−115 m), LP2-M3 in early wear stage with unworn M3.

Distinction from other Maragheh hipparions:

An oval POF well defined all around, located far from the orbit and facial crest; very deep posterior pocket; deep nasal notch with posterior edge situated above P2 mesostyle; orientation of POF horizontal; shallow depression in subnasal area (? subnasal fossa); slender snout intermediate between those of *H. prostylum* and *H. urmiense*; pli caballin double.

Description:

Facial morphology

KNHM PLB-8401 is a female adult skull with canines (APL=10.3 mm; TRNW=6.6 mm) with medium cranial size (Fig. 2). The skull is laterally compressed by postmortem deformation. The IOF is located above the anterior half of P3. The POF begins at the level of the P3 mesostyle and ends at the M2 parastyle. The anterior rim of the orbit is above the M3 metastyle. The nasal notch is retracted to the level of the P2 mesostyle. The POF is located far from the orbit and facial crest (POB=45 mm; FC=30.4 mm) (Figs. 3, 4). Its peripheral margins are well defined, with deep a posterior pocket (depth=20.5 mm) (Fig. 5). The posterior pocket is one of the deepst among the Turolian hipparions. The lacrimal bones enter the POF. A weak ridge oriented antero-ventrally divides the POF into two parts: anterior and posterior. The orientation of the POF is horizontal to slightly anteroventral. There is a shallow depression in the area ventral to the posterior end of the nasal notch. The upper snout is more slender than that of *H. prostylum* and robust than that of *H. urmiense* (=*H. campbelli*) from Maragheh. KNHM W 8659 is a palate and no facial part is preserved. The the anterior rim of choanae is situated to the level of M2-M3 boundary.

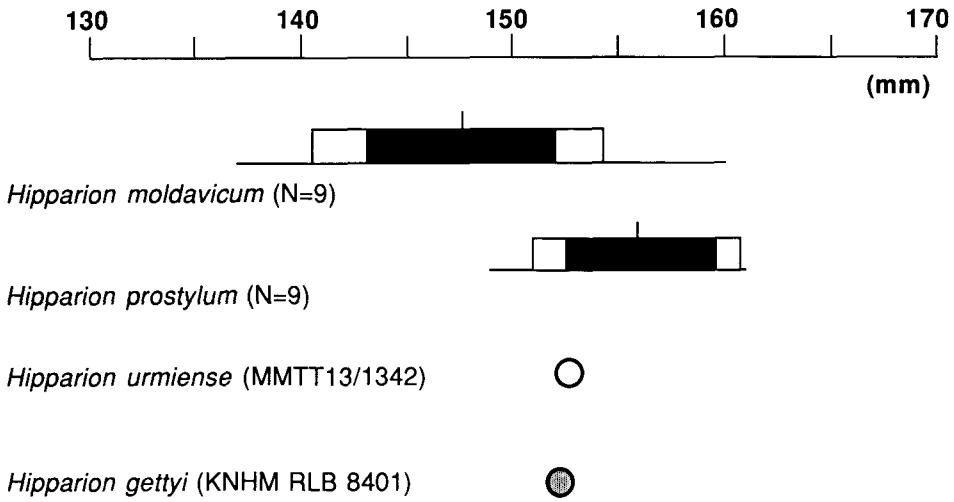

Fig. 2. Dice diagram of the P2-Orbit distance of Maragheh *Hipparion*. Horizontal line represents "range"; vertical line "mean"; open rectangle "mean±1 standard deviation"; and filled rectangle "mean±2 standard errors of the mean (=95% confidence limit of the mean".

Dental morphology

The size of cheek teeth row length is intermediate between those of *H. prostylum* and *H. moldavicum* (P2-M3 occlusal length of *H. gettyi*: 137.3 mm) (Fig. 6). The relative size of the oval protocone is similar to that in *H. prostylum*. The plication counts of the enamel in M1 is higher than the mean of *H. prostylum* and *H. moldavicum* from Maragheh (Fig. 7). The pli caballins are double in both premolars and molars. The plication counts of KNHM PLB 8401 are 14 in M1.

In KNHM W 8659, the pli caballins in the premolars are double, but single in the molars. The protocones of KNHM W 8613 are lenticular in its early stage of wear.

In the very old individuals, KNHM W 86504 and 86505 with very worn teeth, the pre- and postfossettes are very narrow mediolaterally, and the protocone is connected with the protoloph. They give no taxonomic information.

Discussion and compariosons:

The P2-M3 occlusal length (137.3 mm) and P2-Orbit distance (152.3 mm) of KNHM RLB 8401 do not indicate its large size as in other Turolian large forms, e.g. from Pikermi and Samos.

The slender snout and deep posterior pocket of the POF distinguish this form from other Turolian large hipparions, such as *H. brachypys* from Pikermi (Koufos, 1987a, b), *H. giganteum* from Grebeniki, Moldavia S.S.R. (Gromova, 1952; Gabunia, 1959), and large

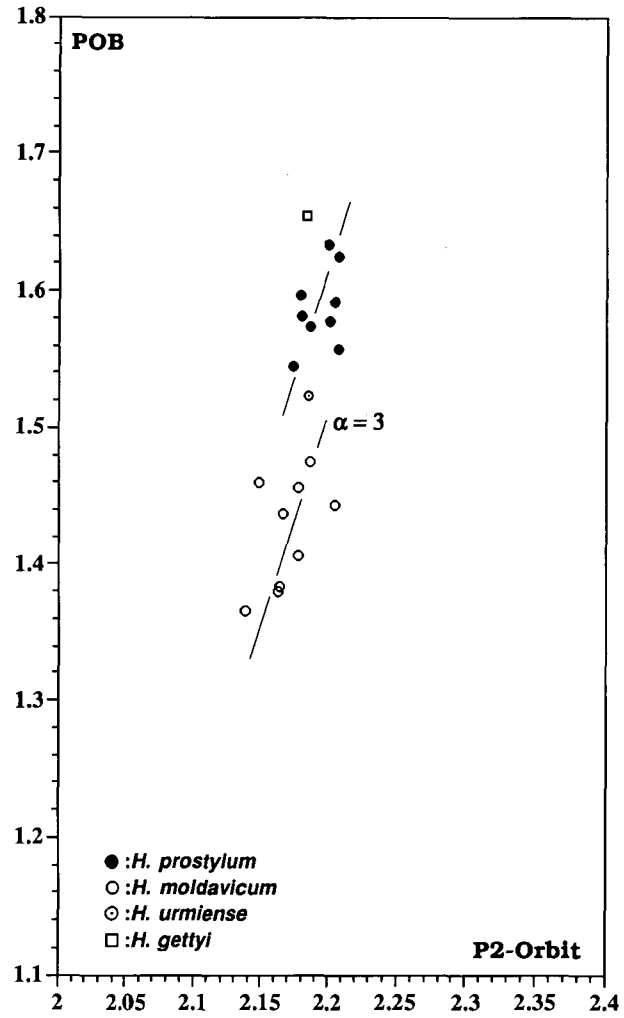

Fig. 3. Preorbital bar width (POB) plotted against the P2-Orbit distance in Maragheh *Hipparion*.
Hypothetical growth line with positive allometry (slope=3) were drawn for *H. prostylum* and *H. moldavicum*.

Hipparion sp. from Samos (SONDAAR, 1970; FORSTÉN, 1980b).

BERNOR (1985) considered this form as ancestral to *H. prostylum*, supposing a phylogenetic hypothesis of a direct ancestor-descendant relationship among *H. gettyi*, *H. prostylum*, and *H. campbelli* (=*H. urmiense*) in anagenetic order.

The facial morphology of *H. getty* is similar to that of *H. prostylum* (Fig. 8).

Hipparion gettyi is different from *H. prostylum* by the following characters;

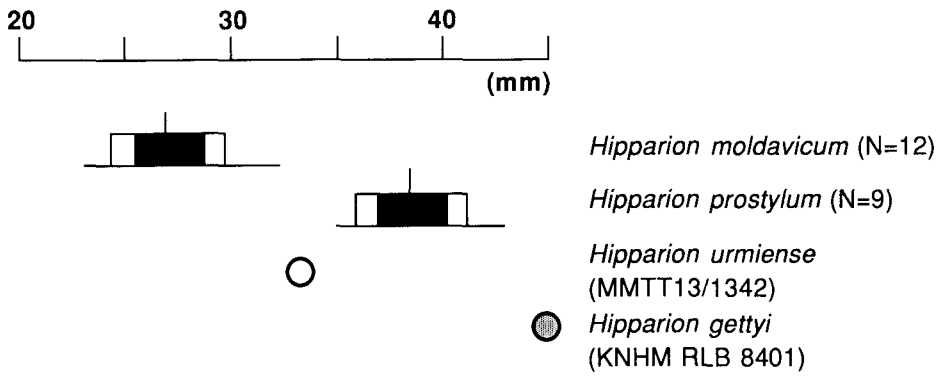

Fig. 4. Dice diagram on the preorbital bar width of Maragheh *Hipparion*.

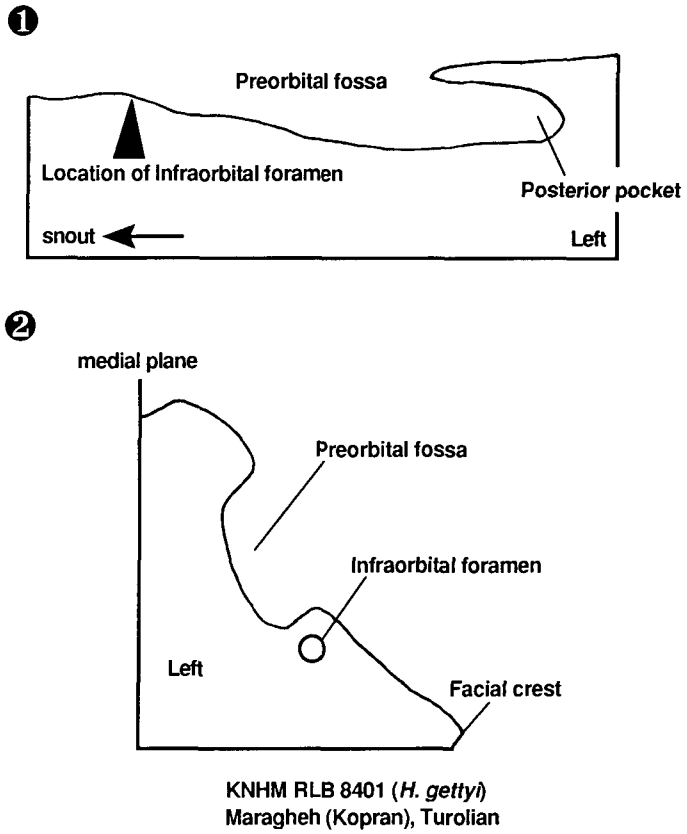

Fig. 5. Anteroposterior (1) and dorsoventral (2) section of the preorbital fossa (POF) of KNHM RLB 8401 (*H. gettyi*, type specimen).
This specimen shows very deep posterior pocket.

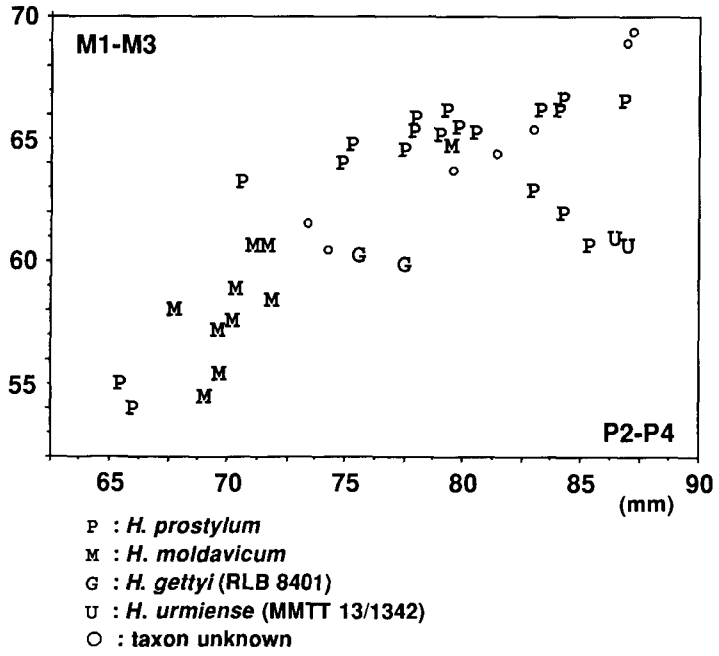

Fig. 6. Molar row length plotted against premolar row length in Maragheh *Hipparion*.

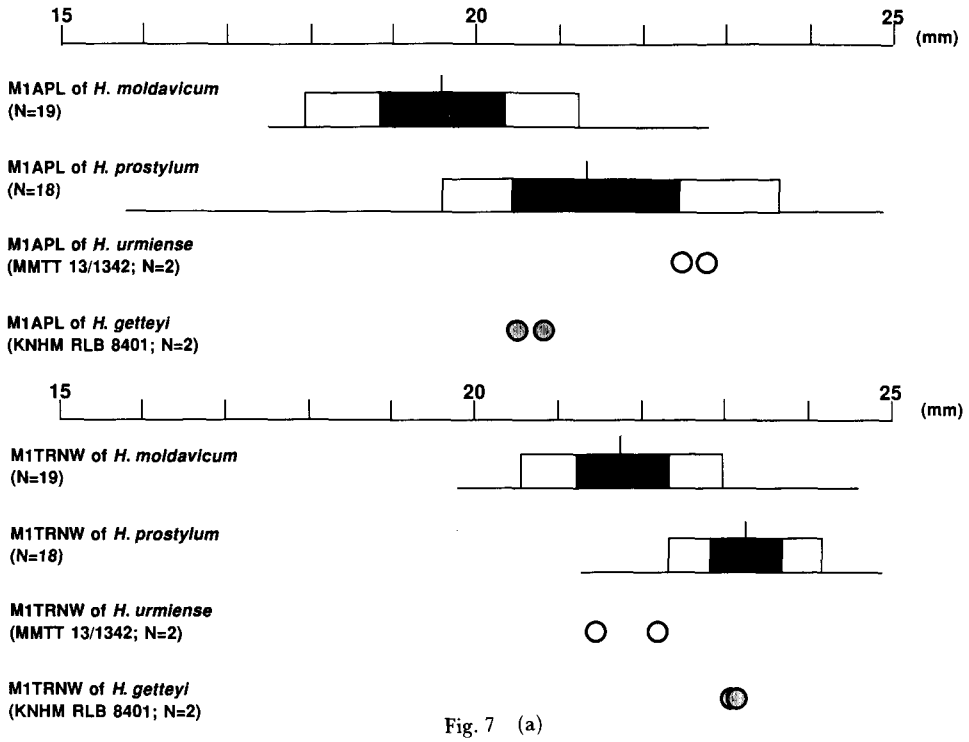

Fig. 7 (a)

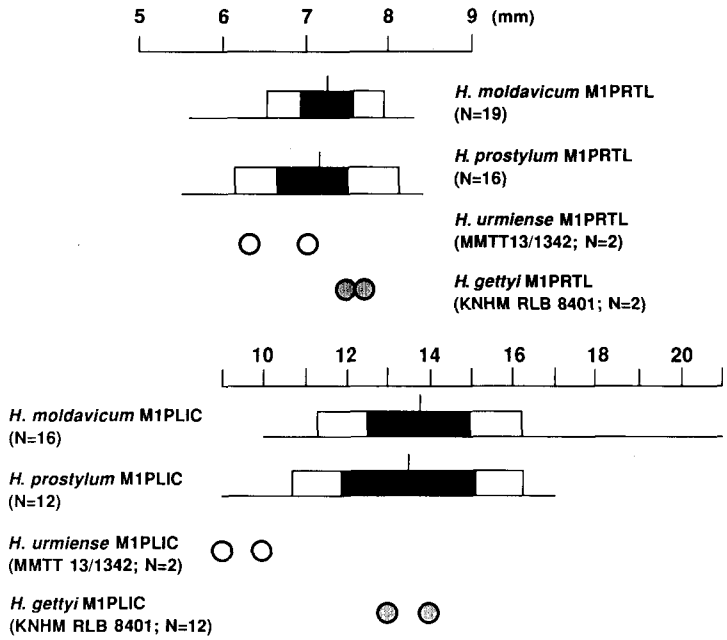

Fig. 7 (b)

Fig. 7. (a) & (b) Dice diagrams for some measurements on M1 in Maragheh *Hipparion*. APL: Anteroposterior length; TRNW: Transverse width; PRTL: Protocone anteroposterior length; PRTW: Protocone transverse width; PLIC: Plication counts of the first molar.

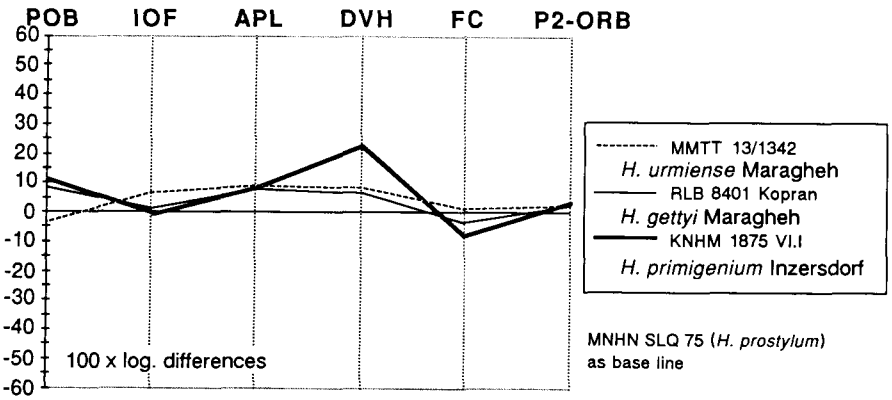

Fig. 8. Ratio diagram on *H. gettyi* from the Kopran sub-locality, *H. urmiense* from UC13 sub-locality, and *H. primigenium* from Inzersdorf (Austria). Inzersorf (Austria) is of early Vallesian in age.

1) Narrower snout, although the only measurable skull is the type specimen and we do not know the individual variation of this character.

2) Deeper posterior pocket, up to 20.5 mm. If the parts of the maxilla and lacrimal

bones overhanging the POF, forming the deep posterior pocket, would be removed, the POB length could become nearly 24.5 mm (=45–20.5: here, the former is the POB, and the latter the posterior pocket depth). This value is quite close to that of *Hipparion moldavicum* and *H. mediterraneum*.

3) The postcranial elements, especially the metapodials, from the Kopran sub-locality assigned to *Hipparion gettyi* are of medium-sized and slender. The size and proportions of the postcranials from Kopran are similar to those of *H. moldavicum* and distinct of those of *H. prostylum* in Maragheh of large-sized and robust proportions (for discussion on cranial-postcranial association see below).

On the basis of these characters of the Kopran hipparion, we present an alternative hypothesis that *Hipparion gettyi* shared a common ancestor with *H. moldavicum* from Maragheh, rather than with *H. prostylum*.

This hypothesis of a *H. gettyi-H. moldavicum* relationship in Maragheh requires the following evolutionary steps (Fig. 9):

1) Reduction of the overhanging part of the maxilla-lacrimal bone, leading to a shortening of the POB. This increases the antero-posterior length of POF from 59.6 mm to 80.1 mm. The APL of POF in *H. moldavicum* from Maragheh close to 80 mm as exhibited by MNHN MAR 1477 (POF APL=78.9 mm), the maximum value among the specimens.

2) Reduction of the enamel plication of upper cheek teeth. The pli caballins in the

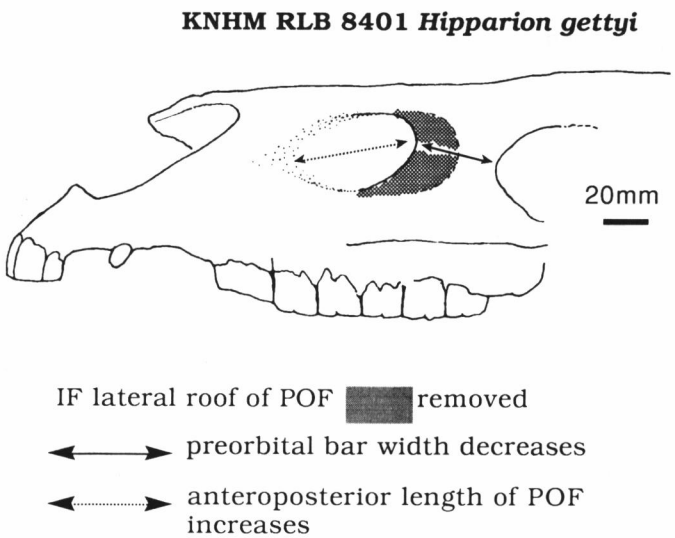

Fig. 9. Modification of facial structure of *H. gettyi*. If the overhanging roof of the posterior pocket in the preorbital fossa is removed, the length of the POF increases and the width of preorbital bar decreases, showing similar morphology to that of *H. moldavicum* and *H. mediterraneum*.

molars became dominantly single and the plication counts in the posterior wall of the prefossette and anterior wall of the postfossette decreased.

The alternative hypothesis by BERNOR (1985) requires the following steps:

1) Increase of snout robustness in *H. prostylum*. The snout of *H. prostylum* is more robust than that of *H. moldavicum*. The robust snout seen in *H. prostylum* is derived characters state among the Vallesian and Turolian hipparions in Eurasia.

2) Reduction of the rim definition of POF in *H. prostylum*.

3) Reduction of the posterior pocket depth.

4) Reduction of the enamel plication counts of cheek teeth. The plication counts of the enamel in *H. prostylum* of Maragheh is not largely different from those in *H. moldavicum*.

5) Change of the proportions of the metapodials and sizes of the tarsal elements. *Hipparion prostylum* from Maragheh has large and robust metapodials corresponding to its larger skull and dental size.

Little has been known about the intermediate and transitional forms between large Vallesian hipparion, such as *H. primigenium* and *Hipparion mediterraneum-moldavicum* forms.

Intermediate forms between *H. prostylum* and *H. moldavicum* on the POB/P2-Orbit scatter diagram and shape of POF have been mentioned by Forstén (1983) from Cimislia and Tudorovo of Moldavia S.S.R. A species *Hipparion tudorovense* has a POF with rounded rhomboid outline and weakly defined rims except the posterior. Some of the Cimislia *Hipparion* have triangular to pear-shaped POF with well defined rims (FORSTÉN, 1983).

Hipparion gettyi is similar to the Vallesian large hipparions in its location and shape of POF (Fig. 8), but its smaller skull size and very deep posterior pocket of POF distinguished it from the latter. It is possible that *Hipparion gettyi* is an endemic form peculiar to Maragheh, which has derived *Hipparion mediterraneum-moldavicum* forms.

Hipparion moldavicum GROMOVA, 1952

Synonymy:

Hipparion mediterraneum, FORSTÉN (1968) (in part)

Hipparion moldavicum, FORSTÉN (1980a)

Hipparion sp. Group 2, WOODBURNE and BERNOR (1980)

"Turolian hipparions with the POF placed close to the orbit" from Maragheh, a part, FORSTÉN (1983)

Hipparion aff. *moldavicum*, BERNOR (1985)

Type: A skull, PIN 1256/3639

Locality: Bender district, Taraklia, Moldavia S.S.R.

Age: Meotian (Turolian, late Miocene)

Grographic range: northern shore of the Black Sea, northwest Iran

Originally referred specimens: All materials of *Hipparion* from Taraklia, in the collection of PIN (no. 1256), except for two skull of *H. platygenys* and large bones, enumerated as "*Hipparion* sp. nov.?".

Maragheh specimens: (Skulls)-MNHN (Paris): MNHN MAR 62 (=RLB 7915) (−52 m/−28 m), adult skull with LP2-M3; MNHN MAR 466 (=RLB 8002) (−52 m/−28 m), adult-old skull with RP2-M3; MNHN 469 (−52 m/−28 m), adult skull with LP2-M3 and RP4-M3; MNHN MAR 1476 (=RLB 8001) (−52 m/−28 m), adult skull with LP3-M3; MNHN MAR 1477 (=RLB 7914) (−52 m/−28 m), adult L&RP3-M3; MNHN RLB 8003 (−52 m/−28 m), old skull with L&RP2-M3; MNHN MAR 66 (=1800), (−52 m/−28 m), adult male skull with snout region (L&RI1-I3, C) and LP2-M2, lacking facial region.

KNHM W 86600 (Ketschawa), adult, maxillar fragment with RP2-M3; KNHM W 86601 (Ketschawa), old skull with RP2-M3; KNHM W 86525 (Ketschawa), nasal-frontal with dorsal rims of orbit and POF.

KYOTO: KUAC 95329 (−20 m), adult-old skull with L&RP2-M3; KUAC 95330 (−20 m), adult skull with P3-M3, RM1-M3.

(Cheek tooth rows): MNHN MAR 1799, very old palate with LP2-M2 and RP2-M2.

The materials in BMNH were not examined.

Original information on the type specimen and variation of *Hipparion moldavicum* by GROMOVA (1952):

The type skull is an old individual with strongly worn teeth, lacking the posterior half of the cranial case, the left zygomatic arch, and the orbit. It was dorso-ventrally crushed and the facial region was obliquely compressed.

Length of the POF is 68–85 mm; height: 41–60 mm; the POB: 20.5–28 mm; FC: 10–28.5 mm in average.

The POF anterior end is located on a level with P3; its posterior end from mid-M2 to the posterior rim of M3. Its shape is approximately an irregular rounded rhomboid. There is a variation in POF shape and in the development of the posterior pocket in the specimens (from no development to 10 mm in depth).

The POF is separated from the buccinator fossa by a clearly uplifted area in most specimens, except no. 6854, in which the POF is united with the buccinator fossa by a small groove.

The development of the POF during the ontogenetic process is traced. The POF in five sub-adult skulls, with M1 and M2 in function but not yet erupted M3, have shorter and lower POF and longer distance from the facial crest in average than aged individuals. The distance of the POF from the orbit (POB) does not change between aged and sub-adult animals.

GROMOVA (1952) pointed out that during ontogeny, the POF became enlarged and deeper, and its peripheral margins became clearer and steeper posteriorly, producing the posterior pocket there.

Diagnosis (Maragheh form):

Medium to small-sized (Fig. 2); rounded triangular POF, centrally located, close to the orbit (Figs. 3, 4); posterior rim of POF high dorso-ventrally; the POF well defined and medially deep; anterior rim of POF exists, the posterior pocket exists (depth: 2.6–7.6 mm); the posterior edge of the nasal notch above the anterior half of P2; the anterior rim of the orbit located at a level with the posterior half of M3 or posterior to the rear of M3 in adults; smaller P2-M3 length, relative to the P2-Orbit distance; protocone rounded to oval; plication counts of enamel 13.1 in average; pli caballins single.

Description:

Skull morphology

The posterior end of the nasal notch is at the level of the anterostyle of P2 in MNHN MAR 62 and MNHN RLB 8003, and not preserved in other specimens.

The IOF is located above the P3 mesostyle in MNHN MAR 62, and at the level of P4 in MNHN PLB 8003, MNHN MAR 1477, MNHN MAR 1476, MNHN MAR 469, KNHM W 86601=RLB 8402, and KNHM W 86600=RLB 8404. In MNHN MAR 466, the IOF is at the level of M1 parastyle, which exists within the anterior part of the POF.

The anterior rim of the POF is located at a level with the P3 (MNHN MAR 62, MNHN PLB 8003, MNHN MAR 1477, and MNHN MAR 466) to the anterior half of P4 (MNHN MAR 1476, MNHN MAR 469, KNHM W 86601=RLB 8402). The posterior rim of the POF is located above the posterior half of M2 (MNHN PLB 8003 and KNHM W 86600=RLB 8404) and above M3 (MNHN MAR 62, MNHN MAR 1477, MNHN MAR 1476, MNHN MAR 466, MNHN MAR 469, and KNHM W 86601=RLB 8402).

The shape of the POF is rounded rhomboid. The POF is well defined in all margins and medially deep. It is situated close to the orbit and the facial crest. The definition of the rims is variable from specimen to specimen. The ventral rim is poorly defined in MNHN MAR 469, KNHM W 86601 (=RLB 8402), KNHM W 86600 (=RLB 8404), and KNHM W 86525. The POB width is short (mean=26.5 mm, N=9) in this form relative to *Hipparion prostylum*. The POB in KNHM W 86525 is 27.0 mm showing this specimen belongs to *H. moldavicum*. The longer axis of the POF is anteroventrally

oriented. The posterior posket of the POF varies in its depth, however, it exists in all specimens. In some specimens (MNHN MAR 62=RLB 7915, MNHN MAR 1477, and MNHN MAR 62), the POF is divided into two parts, anterior and posterior by a crest extending in the direction from posterodorsal to anteroventral in the middle part of the POF. For MNHN MAR 1476, a rather deeper area is seen in posterodorsal part of the POF (foramen fossa sensu SEFVE, 1927). There is no such crest in the POF for MNHN MAR 466 and KNHM W 86601=RLB 8402. The depression continues from the posterior rim of the POF in the malar part to near the facial crest (MNHN MAR 1476). The anterior part of the lacrimal bone is included in the posterior part of the POF, forming the "roof" of the posterior pocket.

The anterior rim of the orbit is located relatively posteriorly to the cheek teeth row. It is above the posterior half of M3 (MNHN RLB 8003 and KNHM W 86600=RLB 8404), or far posterior to M3 (MNHN MAR 62, MNHN MAR 1477, MNHN MAR 466, MNHN MAR 1476, MNHN MAR 469, and KNHM W 86601=RLB 8402).

There is a faint depression anterior to the POF and dorsal to the buccinator fossa, in the position posteroventral to the posterior part of the nasal notch where the subnasal fossa exists in *H. mediterraneum* (MNHN MAR 1476 and MNHN MAR 466). In MNHN MAR 469, the definition of the depression is greater than those seen in other specimens, and similar to the subnasal fossa of *H. mediterraneum* from Pikermi (MNHN PK 262) in its degree of definition and location.

The anterior rim of the choanae is at a level with M1-M2 boundary (MNHN MAR 1477) to M2 (MNHN MAR 62, MNHN RLB 8003, MNHN MAR 1476, MNHN MAR 466, MNHN MAR 469, KNHM W 86601=RLB 8402, and KNHM W 86600=RLB 8404).

The length of cheek teeth row and P2-Orbit distance of this specimens are larger than that of other members of *H. moldavicum* from Maragheh. The P2-M3 occlusal length of MAR 469 is 144.5 mm and P2-Orbit distance ca. 160 mm. This is the largest among Maragheh *H. moldavicum* specimens comparable to the larger specimens of *Hipparion prostylum* from Maragheh.

Among the specimens assigned to *H. moldavicum*, MNHN PLB 8003 and KNHM RLB 8404 have a small P2-Orbit distance compared with the rests. KNHM RLB 8003 was mentioned by FORSTÉN (1983) as falling close to the 95% ellipse, calculated on the data of *H. matthewi* from Samos.

Description of Kyoto University specimens

KUAC 95329 lacks the anterior part of the facial region and snout. The brain case is also missing. The IOF is at the level of the anterior half of P4. The anterior part of the POF is not preserved, and the posterior rim is located above the M3 parastyle. The anterior rim of the orbit is situated far behind M3. The POF is well defined post-

eroventrally but less so dorsally. It is medially deep with an anteroventral orientation. The depth of the posterior pocket is 3.9 mm. There is no crest within the POF dividing it. The lacrimal bone touches the posterior end of the POF. The anterior rim of the choanae reached to the anterior half of M2.

KUAC 95330 is a skull similarly preserved to 95329. The POF is medially deep and defined in all margins. The depth of the posterior pocket is 4.4 mm. The POF is divided into three parts by ridges: dorsal, ventral, and posterior parts blending with the posterior pocket.

Dental morphology

The cheek teeth of *H. moldavicum* from Maragheh are smaller than those of *H. prostylum* from this locality (see description of *H. prostylum* in this paper) (Fig. 6, 7). The relative size of the protocone to overall tooth size in *H. noldavicum* of Maragheh is large compared with that in *H. prostylum* from this locality.

The enamel plication formulae of upper cheek teeth of *Hipparion moldavicum* from Taraklia (CROMOVA, 1952) are as follows: (2–6.5)-(2–8)-(1–4.5)-(0–2)/1–3.5, (total counts: 5–21) in middle worn P4 (N=16); (0–7.5)-(2–8.5)-(1–8.5)-(0–2.5)/0–3.5, (total counts: 3–27) in middle worn M1 (N=25). The average of total plications of P3 to M2 in wear stages for *H. mediterraneum* from Pikermi is 18.8±1.13 (FORSTÉN, 1983). The enamal plication formulae of Maragheh *H. moldavicum* are as follows: (1–5)-(4–9)-(4–7)-(1–2)/1–2, (total counts: 10–23) in middle worn P4 (N=7); (1–5)-(5–8)-(1–7)-(1–3)/1–1, (total counts: 8–23) in middle worn M1 (N=7). The plication counts of Maragheh *H. moldavicum* are similar to those of Taraklia form. The pli caballins are generally single in both premolars and molars, but there are some premolars with a double pli caballin. Neither is the depth of the hypoconal groove different from that of *H. prostylum* of the same locality.

The P2-M3 occlusal length of *H. moldavicum* relative to P2-Orbit distance is smaller than that of *H. prostylum* in Maragheh. This may be caused by the more posterior location of the orbit relative to the cheek teeth row in *H. moldavicum* than in *H. prostylum.*

Comparison and Discussion:

Hipparion moldavicum from Maragheh is similar to *Hipparion mediterraneum* from Pikermi in several features such as: location of the POF close to the orbit and facial crest; well defined periphery of the POF; medially deep POF; its triangular shape (Fig. 10).

In the POB/P2-Orbit scatter diagram (Fig. 3), most skulls of Maragheh *H. moldavicum* fall with in the ellipse of Taraklia *H. moldavicum* together with Pikermi *H. mediterraneum* (FORSTÉN, 1983). Two skulls, KNHM W 86600=8404 and MNHN PLB 8003 with smaller size plot inside the ellipse of *Hipparion matthewi* from Samos.

The statistics of the P2-M3 occlusal length and P2-Orbit distance of the adult skulls of

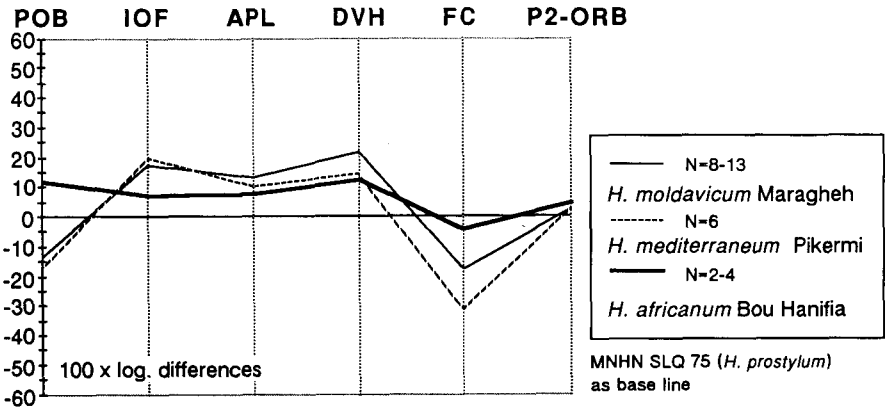

Fig. 10. Ratio diagram on *H. moldavicum* from Maragheh and *H. mediterraneum* from Pikermi (Greece), and *H. africanum* from Bou Hanifia (Algeria). Bou Hanifia (Algeria) is of early Vallesian in age, and Pikermi of middle Turolian.

the Maragheh form are as follows: mean=133.2 mm, C.V.=5.84, N=4 on P2-M3 length; mean=149.7 mm, C.V.=4.49, N=6 on P2-Orbit distance. The adult skulls involved in this analysis are as follows: KNHM W 86600=RLB 8404, MNHN MAR 62, MNHN MAR 466, MNHN MAR 469, MNHN MAR 1476, MNHN MAR 1477, and KUAC 95330. Simple interpretation of these values of the coefficient of variation (C.V.) of the measurements is that these skulls belong to a single species. But the C.V. s of the measurements including all adult skulls from Maragheh, ignoring the difference of their facial morphology, are 5.97 on P2-M3 length and 4.26 on P2-Orbit distance. These values of C.V. are still well within the limits of measurements on single species. This suggests that the C.V. alone does not necessarily reflect the variation of a single species, when specimens from different species of similar size are included.

MELADZE (1967) described *Hipparion* from Bazalethi of Gruzia S.S.R. under the name of *Hipparion garedzicum*, originally described by GABUNIA (1959) on the specimens from Udabno of Gruzian S.S.R. (type skull, MG 156/13), which are geographically and chronologically near to Maragheh. He mentioned five skulls from the same block of a bed of the Dushet Formation in northern Karsimaant-Kari of the Dushet district. The age of the formation is Late Miocene.

Among the five skulls one specimen, B-51, is well preserved with well developed deep POF close to the orbit and the facial crest (POB=31.5 mm; FC=18 mm). The peripheral margins are well defined and there is a posterior pocket. It has a subnasal fossa anterior to POF, separated by a marked ridge from the latter. A second specimen, B-53, lacks the subnasal fossa. The posterior rim of the nasal notch is located above the mid of P2.

There is another hipparion form with a smaller and lower POF located dorsally and

far from the orbit (B-53 and 50: noted in the section of *H. prostylum*) (FORSTÉN, 1983). MELADZE (1967) considered the difference in the facial morphology (shape, size, and location of POF) seen in the Bazalethi hipparions due to sexual dimorphism. However, this can not be supported by our data. The facial morphology of B-51 from Bazalethi is closely related to that of the "*Hipparion mediterraneum*" group.

The hipparions of the "*H. mediterraneum*" group with characteristic facial morphology are distributed in southern Greece, northwest Iran, the Caucasus, and the northern shore of the Black Sea in the late Miocene (Turolian) period. In this group, are included *Hipparion mediterraneum* of Pikermi, Greece; *H. moldavicum* of Maragheh, in Iran, Taraklia, and Novo-Elizavetovka, Tudorovo, and Novaja Emetovka in Moldavia S.S.R., and a part of *H. garedzicum* of Bazalethi, Cruzia S.S.R.

Hipparion prostylum GERVAIS 1849

Synonymy:

Hipparion mediterraneum, FORSTÉN (1968) (in part)

Hipparion sp. Group 3, WOODBURNE and BERNOR (1980)

Hipparion prostylum, MACFADDEN (1980)

"hipparion with the POF placed far from the orbit" from Maragheh, part, FORSTÉN (1983)

Hipparion prostylum (s.l.), BERNOR (1985)

Type: Skull BMNH M 33603 (lectotype by BERNOR, 1985)

Locality: Mt. Luberon, Rhone Valley, southern France

Age: Turolian

Geographic range: southern France, Greece, northwest Iran.

Referred specimens from Maragheh: (SKULL)-WIEN: KNHM A 4844 (Kara Kend), young maxilla with L&RP2-M3; KNHM A 4847 (Kara Kend: −52 m/−28 m), very young male skull with LP2-P4 and RP2-M3 (M3 erupting in alveolus); KNHM A 4848 (Zab Baschi), old maxilla with LP2-M3; KNHM A 4861 (sub-loc.?), adult skull with L&RP2-M3; KNHM W 86515 (Ketschawa), maxilla with LP-2M3 in rock matrices; (?) KNHM W 86526 (Ketschawa), anterior part of the maxilla with LP2-P3 of an adult individual; (?) KNHM W 86527 (Ketschawa), middle part of young maxilla with LP4-M1.

PARIS: MNHN MAR 71 (−52 m/−28 m), adult skull with L&RP2-M3; MNHN MAR 359-1475 (−52 m/−28 m), adult male skull with L&RP2-M3; MNHN MAR 465

(−52 m/−28 m), very old skull with L&RP2-M3; MNHN MAR 1474 (=18), (−52 m/−28 m), old male skull with LP2-M3 and RP2-M2; (?) MNHN MAR 1796, juvenile skull with LDP2-DP4, M1; MNHN MAR 1804 (−52 m/−28 m), adult-old maxilla with RP2-M2.

KYOTO: KUAC 95331 (−20 m), young adult skull with L&RP2-M3; (?) KUAC 95333 (−20 m), young adult maxilla-palate with LP2-M3 and RP2-M2; KUAC 95334 (−20 m), very young maxilla with LP2-P4; KUAC 95045 (−20 m) very young maxilla with RP1, P2-M2; KUAC 95089 (−20 m), adult female (5–6 year in recent *Equus*), skull lacking canines with L&RI1-I3, P2-M3; KUAC 95090 (−20 m), adult male skull with LI3, L&RC, P2-M3.

(Cheek teeth rows)-WIEN: KNHM A 4850 (Ketschawa), adult LP2-M3; KNHM W 8614 (Ketschawa), adult with RP2-M3; KNHM W 8619 (Ketschawa), old with P2-M1; KNHM W 8658 (?), adult LP2-P4; KNHN A 4853 (?), young adult RP2-M3; PARIS: MNHN MAR 1798, very young adult with LP2-M2 and RP3-M2; KYOTO: KUAC 95040, adult maxilla with LP2-M3; KUAC 95042, young RP4-M3; KUAC 95043, young adult LP1, P2-M2; KUAC 95086, young adult LP2-M3, RP4-M1.

Distinctions from other Maragheh hipparions:

Medium to large size (Fig. 2); an oval POF placed dorsally on the facial region, far from the orbit (Fig. 3, 4); anterior rim of POF poorly defined or lacking; dorsal and ventral rims of POF also poorly defined in some cases; well defined posterior rim of the POF often seen as "pit"; poor development of a posterior pocket; snout robust; the posterior edge of nasal notch above the P2 anterostyle or anterior to it; upper first and second incisors arranged straight transversely in middle wear stage; large P2-M3 length; small protocones to tooth size; protocone oval to rounded; plication counts of the enamel 14 in average; pli caballins generally single to double (average of its number from P2 to M2 of young to adult individuals: 1.31; its average in M1: 1.59).

Description of the Maragheh specimens in other institutes:

Facial morphology

One of the characteristic features of this taxon is a robustness of its snout. This is caused by shorter snout length in this taxon than in *H. moldavicum*. The preserved snouts have robust proportions (KNHM A 4847, MNHN MAR 359–1475, MNHM MAR 1474).

The posterior edge of the nasal notch is located above the anterior half of P2 (KNHM A 4847 and MNHN MAR 359–1475). In MNHN MAR 465, it is situated anterior to P2. This was caused by proceeded teeth wear diminishing its anteroposterior length.

The IOF is above P4 (KNHM A 4844, KNHM A 4848, KNHM A 4861, MNHN MAR 71, MNHN MAR 359–1475, MNHN MAR 465, MNHN MAR 1474, MNHN MAR

1804) or above the posterior half of P3 (KNHM A 4847). In KNHM W 86515 and KNHM W 86526, the IOF is at a level with the P3-P4 boundary.

As the anterior rim of the POF are poorly defined, it is difficult to determine its location precisely. Some specimens lack it. It is located at a level with the anterior half of P4 (KNHM A 4847, MNHN MAR 71, MNHN MAR 359–1475, MNHN MAR 465) or P3 (MNHN MAR 1474). The posterior rim of the POF is located at a level of the anterior half of M2 (KNHM A 4847, KNHM A 4861, KNHM W 86515, and MNHN MAR 71), or the posterior half of M2 (MNHN MAR 359–1475 and MNHN MAR 1474). In MNHN MAR 465, it is above the M3 parastyle. The dorsal, ventral, and posterior rims of the POF are variably defined. The POF is well defined in the posterior and ventral rims and medially deep (KNHM A 4847, KNHM A 4844, KNHM A 4848, and MNHN MAR 359–1475). The ventral rim of the POF is often poorly defined (KNHM A 4861, KNHM W 86515, MNHN MAR 71, MNHN MAR 465, MNHN MAR 1474, MNHN MAR 1796). The longer axis of POF is anteroposteriorly oriented.

The POF is located far from the orbit and the facial crest. The distance (FC) between the ventral rim of the POF and the facial crest is 31.5 mm in KNHM A 4844; 26.1 mm in KNHM A 4848; and 30.6 mm in MNHN MAR 1804. The POB width is 38.6 mm in average (N=9). The posterior pocket develop variously in specimens. In KNHM A 4847 and KNHM A 4847, there is a foramen fossa (sensu SEFVE, 1927) and the depth of the posterior pocket is 8.5 mm in the former. The depth of the posterior pocket is 2.2 mm in MNHN MAR 359–1475. In MNHN MAR 71 and MNHN MAR 1474, there is a well defined "pit" in the posterior margin, but no posterior pocket. There is a weak ridge running anteroventrally within the POF, dividing it into anterodorsal and posteroventral parts (KNHM A 4847, MNHN MAR 71, MNHN MAR 465, and MNHN MAR 1474).

The malar region dorsal to the facial crest is flat and there is very shallow depression (KNHM W 86527, MNHN MAR 359–1475, and MNHN MAR 1474). The facial crest ends anteriorly at a level with P4-M1 boundary (KNHM W 86527). The lacrimal bone does not reach the posterior rim of the POF.

The anterior rim of the orbit is above the metastyle of M3 (KNHM A 4847, KNHM A 4861, and MNHN MAR 71), or posterior to M3 (MNHN MAR 359–1475, MNHN MAR 465, and MNHN MAR 1474).

The anterior rim of the choanae is at a level with M1-M2 (KNHM A 4844, KNHM A 4847, and KNHM A 4861), or with M2 (MNHN MAR 71, MNHN MAR 359–1475, MNHN MAR 1474).

Dental morphology

The occlusal length of P2-M3 varies from 143.2 mm (KNHM W 86515) to 152.1 mm (KNHM A 4844). It changes by wear. The elder individuals with severe wear condi-

tion have shorter occlusal length of cheek teeth row (120.4 mm in MNHN MAR 465; 133.1 mm in MNHN MAR 1474).

The sex of the specimens can be inferred by their canines size. In the male specimens, the canines are large (APL=12.4 mm, TRNW=8.4 mm in KNHM A 4847; APL=11.2 mm, TRNW=8.3 mm in MNHN MAR 359-1475; APL=10.6 mm, TRNW=8.7 mm in MNHN MAR 1474; APL=9.8 mm, TRNW=8.1 mm in KUAC 95090). KUAC 95089 lacks canine and is considered female. KNHM A 4848 was assigned to *H.* cf. *moldavicum* by BERNOR (1985). The assignment of KNHM W 86526 to *Hipparion prostylum* is tentative.

Description of the specimens in Kyoto University:

Facial morphology

KUAC 95331 is a young adult skull. KUAC 95333 is a young adult maxilla. The skull in general was curshed dorsoventrally (KUAC 95333). The dorsal pat of the facial region is absent. KUAC 95334 is very young left maxilla fragment with P2-P4 in early wear stage (P2 crown height is 50.1 mm). KUAC 95089 is a female adult without upper canines. KUAC 95090 is an adult skull with large canine (APL=9.8 mm; TRNW=8.1 mm), showing male sexuality.

The snout is robust and the arrangement of incisors (I1 and I2) is transversely straight, exhibiting one of the diagnostic characters of *Hipparion prostylum* (KUAC 95089 and KUAC 95090). The posterior edge of nasal notch is above the anterostyle of P2 (KUAC 95089 and KUAC 95090).

The IOF is located at a level with P4 (KUAC 95331, KUAC 95333, and KUAC 95089), or with the P3-P4 boundary (KUAC 95334). In KUAC 95090, it is above the P4-M1 boundary.

The anterior rim of the POF is poorly defined and often unrecognizable. In KUAC 95089, it is above the P4 parastyle, although it is unclear. The posterior rim of POF is well defined and located above the M2 (KUAC 95331, KUAC 95045, KUAC 95089, and KUAC 95090). The POF is located high on the facial region and far from the orbit. The longer axis of the POF is horizontally oriented.

The definition of rims of the POF is variable. The posterior rim of POF is well defined (KUAC 95045, KUAC 95089, KUAC 95331, and KUAC 95333). The ventral rim is well defined in KUAC 95331, although it is poor in KUAC 95045. The POF shown as shallow depression is dorsally located and poorly defined all around in KUAC 95090. There is the foramen fossa (sensu SEFVE, 1927), and the depth of the posterior pocket is 5.3 mm in KUAC 95331. Shallow pocket with depth less than 1.0 mm exists in KUAC 95089. There is a clearly marked pit in the posterior rim of POF in KUAC 95090. The is a faint anteroventrally oriented crest within the POF dividing it into posteroventral and anterodorsal parts (KUAC 95331 and KUAC 95089).

The lacrimal bone does not touch the posterior rim of the POF (KUAC 95331, KUAC 95089, and KUAC 95090). The anterior rim of the orbit is at a level with the posterior half of M3 (KUAC 95331, KUAC 95089, and KUAC 95090), or posterior to M3 (KUAC 95045). The anterior rim of the choanae reached to the level of the anterior half of M2 (KUAC 95331 and KUAC 95090), or the M1-M2 boundary (KUAC 95089). In KUAC 95333, it is retracted to the level of M2-M3 boundary.

In KUAC 95045 only the posteroventral part of the POF is preserved. The ventral and posterior rims of the POF are well defined and situated far from the facial crest and the orbit respectively (FC=32 mm). There is a posterior pocket, but of unknown depth due to rock matrix. The IOF is located at a level with the posterior half of DP3. The lacrimal does not touch the POF.

Dental morphology

The cheek teeth series of *H. prostylum* can be distinguished from those of *H. moldavicum* from the same locality by their greater length (Fig. 6, 7). The mean value of the cheek teeth row length of *H. prostylum* is 145.9 mm (N=9), and that of *H. moldavicum*, 129.4 mm (N=7). The occlusal length of P2-M3 varies from 142.7 mm (KUAC 95090) to 146.7 mm (KUAC 95089).

There is no significant difference in the protocone size of M1 between the two forms, but the size of M1 of *H. prostylum* is larger than that of *H. moldavicum* (mean M1TRNW: 23.1 mm, N=17 on *H. prostylum*; mean M1TRNW=21.5 mm, N=15 on the latter form). Thus, *Hipparion prostylum* has a smaller protocone relative to tooth size than *H. moldavicum*.

The plication counts of this form are not largely different from those of *H. moldavicum*. The pli caballins are double, often single in moderately worn premolars and single, often double in the molars. It is difficult to differentiate this form from *H. moldavicum* solely on the basis of occlusal morphology, without using their dimension. The dimensions of the teeth and their relative protocone size are more suitable criteria for this purpose (but not the best).

Comparison and Discussion:

Hipparion prostylum is dominant among the hipparions from Maragheh. This form is larger than *H. moldavicum* in its cheek teeth row length and P2-Orbit distance (skull size) (Figs. 2, 3, 11). The species has wider POB than *H. moldavicum* (Fig. 11). *Hipparion prostylum* was originally described from Mt. Lebéron of the Rhone Valley, southern France. The form exhibits a characteristic robust (short) upper snout.

In the northern shore regions of the Black Sea in U.S.S.R., there is a form of which the relative distance of the POF from the orbit is intermediate between *H. prostylum* and *H. mediterraneum-moldavicum*: *Hipparion verae* from Grebeniki, Moldavia S.S.R. (originally described by GABUNIA, 1959, as *H. gromovae*, but that name has already been used for a

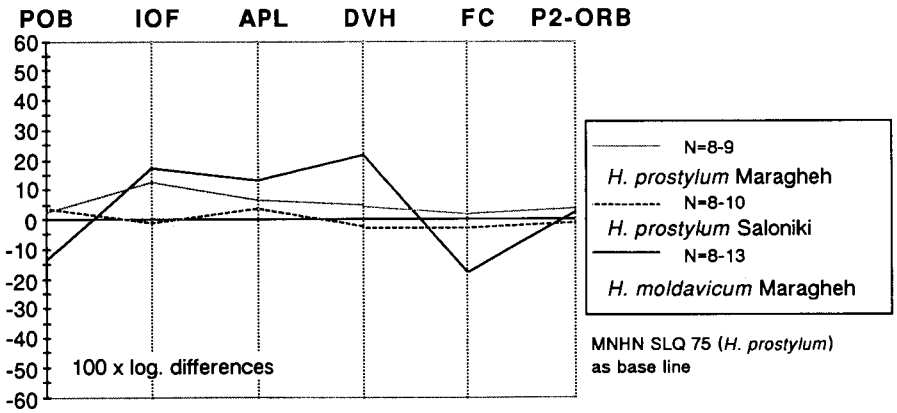

Fig. 11. Ratio diagram on *H. prostylum* from Maragheh and Saloniki (Greece) and *H. moldavicum* from Maragheh. Age of Saloniki (Greece) is Turolian.

Spanish hipparion). Some hipparions from Cimislia and Tudorovo of Moldavia S.S.R. are also similar to *H. prostylum* in the POB/P2-Orbit scatter diagram (FORSTÉN, 1983).

Hipparion verae has a P2-M3 length 131–155 mm. The mean distance of POB from the orbit is 34 mm (GABUNIA, 1959). The shape of the POF is oval and its rims are weakly defined, except the posterior one. The location indices of POF to the orbit and facial rest are 51.5–71.1, and 60.3–76.8, respectively (GROMOVA, 1952). The values of the indices are intermediate between *H. mediterraneum* of Pikermi and *H. prostylum* of Saloniki. Wide snout of *H. verae* (GABUNIA, 1959) shows similarity to that of *H. prostylum.*

Hippparion tudorovense GABUNIA (1959) is a medium-sized form with a P2-M3 length 126–137 mm. The POF is deep and rounded rhomboid shape, similar to that of *H. moldavicum* (FORSTÉN, 1983). The location indices to the orbit and facial crest are respectively 54–59.6 and 47–58.2 (GABUNIA, 1959). Although the POF morphology of *H. tudorovense* is similar to tht of *H. moldavicum,* there are some specimens plot within the ellipse of *H. schlosseri* from Samos in the POB/P2-Orbit scatter diagram (FORSTÉN, 1983, fig. 5).

Although mentioned forms, *Hipparion verae* and *H. tudorovense* are certainly directly comparable with *H. prostylum,* their shape and location of POF shows an intermediate placement between *H. moldavicum* and *H. prostylum* (FORSTÉN, 1983, fig. 4 and 5).

The hipparions from Cimislia in Moldavia have been described by BARBU (1959). The POB is 31–40 mm, and 35.8 mm in average. The POF length and height are 60.1 mm and 36.5 mm, respectively. The location index to the orbit is 60 and the value is close to that of *H. prostylum.* The shape and location of POF shown by BARBU (1959; fig. 3, p. 20; fig. 6, p. 24) are similar to those of *H. prostylum.* However, the relative location of their POF is variable and some specimens are similar to *H. moldavicum.* Probably, there are at least two forms in Cimislia specimens. The length of P2-M3 of Cimislia hipparions is 136 mm. The nasal notch is not extracted posterior to P2 anterior margin.

Hipparion garedzicum mentioned by MELADZE (1967) from Bazalethi in Gruzia S.S.R. is heterogeneous in its facial morphology. MG 50 has the POF with only posterior rim well defined which is placed far from the orbit (POB=45 mm). The P2-M3 length of all specimens ranges 137–158.5 mm. In MG 50, the nasal notch ends above the anterior tip of P2. The location indices to the orbit and facial crest in the specimen are 75 and 95.7 respectively. These values are similar to those of *H. prostylum* (Saloniki, MHHN SLQ 74; 78 and 100; *H. dietrichi* from Samos, KNHM A 4765: 77.3 and 104.9), and *H. gettyi* from Kopran sub-locality of Maragheh (KNHM unnumbered: 75.5 and 93.5). The mean values of the two indices on *H. prostylum* of Maragheh (N=8) are 67.5 and 114.6 respectively. A comparison should be made between Maragheh *H. prostylum* and *H. garedzicum* from Bazalethi, Gruzia S.S.R. and hipparions from Cimislia, Moldavia S.S.R. that are closely located geographically in the Sub-Paratethys region to which Maragheh belongs.

The hipparions with POF more or less reduced (especially in anterior rim definition), dorsally located, and situated far from the orbit are present at other localities of Eurasia (e.g., *Hipparion antelopinum* from the Siwalik; BERNOR and HUSSAIN, 1985; hipparions from Turolian sites of northern China: FORSTÉN, 1983; QIU et al., 1987).

Hipparion urmiense GABUNIA 1959

Synonymy:

Hipparion mediterraneum, FORSTÉN (1968) (in part)
Hipparion campbelli, BERNOR (1985)

Type: A fragment of a skull, MG no. 148/191, and the materials collected from Maragheh, preserved at Muzei Gruzii, Tbilisi, Gruzia S.S.R.

Locality: Maragheh, northwestern Iran

Age: lower Pliocene

Geographic range: Iran (Maragheh)

Diagnosis of the species after GABUNIA (1959):

Skull

Medium-sized; relatively large upper cheek teeth row length (147–155 mm) compared with skull size; narrow skull, with narrow frontal width of lateral edges of orbit (130 mm), width of cranial case at postorbital constriction (about 61 mm), width of nasal bones (either sides) about 85 mm; POF absent or presented with very weakly notice and strongly

moved anteriorly and dorsally as rudiment of lacrimal depression. The width of the preorbital bar is intermediate between those of *H. prostylum* and *H. moldavicum* from the same locality (Fig. 3).

Upper teeth

Relatively large; upper molars relatively small: molar-premolar index 82.1; protocone not elongated: its index of length on weakly or medially worn P3-M2: 26–36.9 (average 30.1), on severely worn 26.2–42 (average 31.5), index of shape 41.1–66.6 (average about 50) and 56–71.5 (average 64.4) one another; the enamel plication of upper cheek teeth weak: plication counts on posterior border of prefossette and anterior border of postfossette of medially-severely worn P3, 4 and M1 in average 2–3.5 and up to 5; cheek teeth height moderate: index of height to length in P3, 4, 230–246; in p3, 4 and m1, 234–258.

Lower teeth

Double knots almost hipparionid type, but in some examples tendency for caballoid type observed; ectoflexid of lower cheek teeth shallow; supplementary dental elements developed weakly; infundibular of i3 remains almost all width of tooth.

Limbs

Extremity bones gracile: index of width in distal end to length of MC III about 12.8; that of MT III about 11.7; lateral digits developed in medium degree: the index of the diameter of distal end in lateral metapodials to medial diameter of distal end of MC III is 64.1, as well as MT II, IV and that of MT III is 61.4; index of the length of first phalange of lateral digits to medial length of phalanges of third digit is 50 in fore limb, 47.4 in hind limb.

Description of MMTT 13/1342 (*Hipparion campbelli* by BERNOR, 1985)

Specimen: A skull, MMTT 13/1342, preserved at the Department of Earth Sciences, University of Califormia, Riverside.

Locality: Shollovend, Upper Maragheh (the horizon of −18 m from the "Loose Chips" bed), northwestern Iran.

Age: Turolian, Late Miocene

Diagnosis of *H. campbellii* (=*H. urmiense*) by BERNOR (1985, p. 206):

"An hipparionine species with a long slender snout; POF markedly reduced, egg-shaped and antero-posteriorly directed, with a small vestigial posterior rim and slight medial depression; preorbital bar moderately long; lacrimal bone placed well posterior to the POF; nasal notch placed above mesostyle of P2; middle wear adult maxillary cheek teeth have moderately complex and very thinly banded plications of the pre- and postfossettes, pli caballins are single, hypoglyphs are moderately deeply incised; pro-

tocones are oval shaped; the P2 anterostyle is elongate; mandibles are elongate with a slender symphysial region; canines are placed immediately distal to i3, mental foramen is placed approximately 1/2 the distance between i3 and p2; in middle adult wear p2 anterostylid is elongate, ectoflexids do not separate metastylids and metaconnids in the premolars, but do in the molars; pli caballinids and ectoparastylids are absent; linguaflexids are shallow; metaconids and metastylids are rounded; metapodials are slender and elongate."

Description (based on a gypsum cast stored in MNHN):

Facial morphology

This is a young female individual with small canines. The anterior part of M3 is in an early stage of wear and posterior part is not in wear. The infundibulars of I1-I2 are fully developed mesiodistally on the occlusal suface. The I3 is erupting and not in wear.

The POF is poorly defined as shallow depression dorsally located on the facial region. There is a well defined posterior pit in the posterior part of the POF. The depression extends dorsally backward beyond this pit. The POB width was measured as the distance between this pit and anterior rim of the orbit. The POF is situated moderately far from the orbit (Fig. 8). There is no posterior pocket. The longer axis of the POF is oriented anteroventrally. The posterior pit of POF is located above the anterior half of M2 and the IOF is above the P4 parastyle. The nasal notch (slit) is retracted at a level with the P2 mesostyle. The anterior rim of the choanae is at the level of the M1-M2 boundary. Developed are a shallow depression in the malar area ventral to the POF depression.

There is a shallow depression ventral to the posterior edge of the nasal notch blending with the buccinator fossa. The location of the depression is similar to that of the subnasal fossa, it was developed in the vacant space of the maxillary bone dorsal to P2 roots. It is difficult to distinguish whether the depression is the postmortem deformation or real biological character.

Dental morphology

According to GABUNIA's (1959) description of *H. urmiense* from Maragheh, the enamel plication in the posterior wall of the prefossette and anterior wall of postfossette counts 2–3.5 to 5 in middle to strong-worn P3-4 and M1-2. The cheek teeth of *Hipparion urmiense* are characterized by low plication numbers of the enamel.

The dental morphology is as mentioned by BERNOR (1985). However, it is rather difficult to distinguish by it this taxon from other hipparions of Maragheh. The occlusal length of the cheek teeth row (148.2 mm) and the P2-Orbit distance (152.7 mm) of MMTT 13/1342 are comparable with those of *H. prostylum* form from Maragheh. As MMTT 13/1342 is a young individual with M3 at early wear stage, the direct comparison

of their dental characters are misleading. The teeth size is as follows; M1TRNW: 21.5, 22.2 mm; and M1PRTL: 6.3, 7.0 mm (left and right) (Figs. 6, 7). The protocones of MMTT 13/1342 are oval, with spur in P3 and P4. The pli caballins are single. The plication formulae in P4 is 5/5/2/1/1 (total: 13); and in M1, 3/3/2/1/1 (total is 9).

Discussion on Synonymy of *Hipparion campbelli* BERNOR (1985) with *H. urmiense* GABUNIA (1959)

Hipparion campbelli (MMTT 13/1342) by BERNOR (1985) was characterized by a narrow snout and frontal part, and strongly reduced POF as a shallow depression dorsal on the facial region. Those features of *H. campbelli* correspond to those of *Hipparion urmiense* GABUNIA (1959).

GABUNIA (1959) described the skull and postcranial materials collected from a site near the village Kyurtevyul in 50 km east from the Lake Urmia (Lazayeh) of Iran. The beds in this locality yielded those materials probably belongs to the Maragheh Formation. The description of the beds yielding the fossils is as follows: sandy clay of dilluvium and streams on the southern slope of Mt. Sahand. The type specimen is a skull fragment, MG no. 148/191, stored in the geological section of the State Museum of Gruzia (Muzei Gruzii). There are other materials assigned to its hypodigms from the same locality. According to GABUNIA's original description, the upper cheek teeth row length of *H. urmiense* is 147–155 mm and the frontal width across the lateral edges of the orbits is 130 mm.

The same measurements on *Hipparion campbelli* (MMTT 13/1342) are 148.2 mm, 146.5 mm in either sides and 131 mm, respectively.

For the other hipparions from Maragheh, there are a few cases in which it is possible to measure the frontal width, because of poor preservation. The frontal width of *H. prostylum* group (KUAC 95090) is 157.5 mm and its cheek teeth row length is 142.1 and 142.7 mm. KUAC 95330, a member of *H. moldavicum*, has a frontal width of about 130 mm.

Though the frontal width of *H. moldavicum* is similar to that of *H. urmiense* and "*H. campbelli*", its facial morphology (shape and location of POF) is quite different from the latter, having a well defined and deep, triangular, POF close to the orbit and the facial crest.

KUAC 95090 is a member of *Hipparion prostylum*, with a relatively more reduced POF than the rests of *H. prostylum* from Maragheh. The hipparion with robust snout and more reduced POF than those of *H. prostylum* from Maragheh is found at Samos as *Hipparion schlosseri-dietrichi* (FORSTÉN, 1983). KUAC 95090 has a wide skull and robust snout similar to those of *H. prostylum* with better defined POF located dorsally on the face. On the other hand, *H. campbelli* has a narrow skull and slender snout, but all are female individuals.

The M1 TRNW in medially worn tooth of *H. urmiense* (GABUNIA, 1959) is 23.5 mm on average. The M1 PRTL is 8.1 mm and total plication counts of M1 are 7.3. The teeth dimensions (tooth width and protocone length) are larger than those of MMTT 13/1342 from Maragheh. The larger dimension of *H. urmiense* by GABUNIA was probably caused partly by that he had included into his hypodigms of the taxon the larger teeth belonging to other forms from the locality (probably to *H. prostylum*).

GABUNIA (1959) mentioned limb elements assigned to his new species. However, it is rather difficult to decide whether the described limb elements really belong to that taxon or not. It is possible that the limb materials examined by GABUNIA are derived from different hipparion forms in Maragheh. The MC III mentioned (ibid.) is longer and slender, close to the large and slender group (WATABE and NAKAYA, this volume).

The dental and facial morphology of *Hipparion campbelli* by BERNOR is close to those of *Hipparion urmiense* GABUNIA (1959). We question about the entity of *H. campbelli* as a new species.

The hipparions with reduced POF have been reported from the Turolian localities: *Hipparion hippidiodus* SEFVE (1927), northern China; and *H. platygenys* GROMOVA (1952), Taraklia, Moldavia S.S.R. As these two forms have no preserved snout region, it is impossible to compare them with the characteristic features of the upper snout in *H. urmiense* from Maragheh.

Hipparion hippidiodus comes from Loc. 115 of Qingyang, Gansu of northern China. The form is of large-sized (M3819 of the Lagrelius collection of Uppsala University, Sweden, P2-Orbit distance 162 mm; P2-M3 occlusal length 146.6 mm). There are no rims of the anterior, dorsal and ventral parts of the POF. The posterior rim is determined by a small well marked pit, located 36 mm anterior to the orbit. A shallow depression is seen in the malar region.

Although the exact width of the skull of *H. hippidiodus* is not measurable it is probably larger than that of *H. urmiense* (the frontal width across the lateral edges of the orbits in M 3819 from Loc. 115 is over 132 mm). M 3818 from Loc. 43 of Baode in the Shanxi province, northern China, is considered as an upper snout of *H. hippidiodus* with large premolars and relatively small rounded protocones. The snout proportions are measurable on the specimen. Its proportions are close to that of MMTT 13/1342, however, the lateral crushing should be considered.

Hipparion platygenys was described by GROMOVA (1952) from Taraklia together with *H. moldavicum*. The type specimen, PIN 1256/2883, has a P2-M3 occlusal length of 150 mm. The reduced POF has only posterior rim. The type skull of *H. platygenys* (PIN 1256/2883) shows the dental dimension such as M1TRNW: 22.0 mm and M1PRTL: 6.1 mm. Those of PIN 1256/2932 are 23.0 mm and 6.3 mm respectively. The plication counts in M1 are 14 for PIN 1256/2883 and 8 for PIN 1256/2932. These values of *H. platygenys* from Taraklia are close to those of MMTT 13/1432 from Maragheh. On the POB/

P2-Orbit scatter diagram presented by FORSTÉN (1983), this form plots close to MMTT13/1342 from Maragheh, falling within the ellipse of *H. moldavicum* from Taraklia (FORSTÉN, 1983, fig. 3). The width measurements on the skull of *H. platygenys* have not been obtained.

KOROTKEVICH (1988) reported a hipparion skull from Cherevichnoe in Ukraina S.S.R. of Meotian age (Photo table 31, p. 63). This specimen (stored in Institute of Zoology, Kiev) named as *Hipparion* sp. exhibits close similarity in its facial morphology to *H. urmiense*. Cherevichnoe is correlated to Tudorovo of Moldavia and included in the MN 13 zone (KOROTKEVICH, 1988).

The specimen is a male with large canines. It has a deep nasal notch with its posterior edge above the P2 posterior half. The POF is a shallow depression with no clear rim. The anterior rim of the orbit is situated above the rear edge of M3. These characters are quite similar to those in MMTT 13/1342. The difference is in overall size and snout length. The P2-Orbit distance of the Cherevichnoe specimen is about 167 mm (from photo table 31 by KOROTKEVICH, 1988, thus approximate) and the percent of the I3-P2 distance to cheek teeth row length is 66.7%. The latter value for MMTT 13/1342 is 50%. The larger overall size of the Cherevichnoe form might affect the snout length (I3-P2 distance).

Another hipparion from Cherevichnoe is named *Hipparion tudorovense*. It has a well defined oval POF situated close to the orbit. The posterior edge of the nasal notch ends at the level of the anterior half of P2. This form is similar to *H. moldavicum*.

Hipparion platygenys from Taraklia (GROMOVA, 1952), *H. urmiense* from Maragheh (GABUNIA, 1959), *H. campbelli* (GERNOR, 1985=*H. urmiense* in this study), and *H. hippidiodus* from Gansu (loc. 115) (SEFVE, 1927) share similar characters in their facial and dental portions. This suggests the monophyletic status of those hipparions with reduced POF, which have been considered as derived in parallel at different lineages (for example, BERNOR, 1985). Further study on these hipparions will possibly solve this problem.

7. Upper Cheek Teeth from Maragheh

Size Distribution of Upper Cheek Teeth Row

The size of the cheek teeth row of the Maragheh hipparions was analyzed in occlusal surface length scatter diagram (Fig. 6). There are two major clusters, consisting of smaller and larger cheek teeth rows. The smaller cheek teeth rows belong to *Hipparion moldavicum*. The larger cheek teeth rows belong to *H. prostylum* and *H. campbelli* (=*H. urmiense* by GABUNIA). There is an overlap of these forms. The young skulls of *H. moldavicum*, with slightly worn M3, show rather large cheek teeth row as is usual in young individuals of *Hipparion*. The premolar row of *H. moldavicum* from Maragheh ranges from 65 to 75 mm in length. In *H. prostylum* and *H. urmiense* from the same locality, it ranges

from 75 to 87 mm.

For the lower cheek teeth row length, there are two size clusters: small rows, with the premolar row ranging from 67 to 75 mm; large teeth rows, with premolar row ranging from 76 to 85 mm. These size clusters on the upper and lower cheek teeth rows correspond well to each other. The smaller upper teeth rows assigned to *H. moldavicum* correspond to the smaller lower teeth rows, and the larger teeth rows of *H. prostylum* and *H. urmiense* to the larger lower teeth row.

The Kopran skull (*Hipparion gettyi*), considered the stratigraphically oldest hipparion in the Maragheh sequence by BERNOR (1985), falls in an intermediate field between the large and small upper tooth rows. In the lower cheek tooth row, the mandibles from the Kopran sub-locality plot separately into large and small forms. KNHM A 4851, with unworn m3, shows large row length, and KNHM A 4846, an adult, has small row length. The large size of the row in A 4851 might be an effect of early wear. The size of the Kopran skull (P2-Orbit distance) is comparable to the upper teeth row length as intermediate between smaller *H. moldavicum* and larger *H. prostylum* and *H. urmiense.*

8. Sorting out of Mandibles from Maragheh

Large cheek teeth row: KNHM A 4845 (Zad Baschi); KNHM A 4866, 4851 (Kopran), KNHM W8612 (Ketschawa); MNHN MAR 73 and 88 (same individual), 63, 456, 457, 463, 464, and 468; KUAC 95039 (Kyoto), KUAC 95337 (Kyoto).

The specimens from Zad Baschi, Kopran, Ketschawa, MNHN, Kyoto collections are included in this group. KNHM A 4845 from Zad Baschi has very large premolar and molar length compared with the rests of mandible, in spite of its moderate wear condition.

Small cheek teeth row: KNHM A 4846 (Kopran); KNHM W 8622 (Ketschawa); KUAC 96077 (Kyoto); MNHN MAR 67, 458, 460, 461, and 462. The specimens from Ketschawa, Kopran, MNHN, and Kyoto collections are included.

The first molar (m1) that belongs to the small sized cheek teeth row and smaller member of large teeth row tend to show relatively large anterior and posterior transverse width of the occlusal surface compared with those of the larger members of large teeth rows. This reflects the fact that in the small cheek teeth row group and smaller member of large teeth row group relatively older individuals are included. The transverse width of the occlusal surface in the lower cheek tooth becomes larger through wear process.

KNHM A 4866 of the large teeth row group is an young individual in which m3 is not in wear. MNHN MAR 73 and 88 belonging to the same individual show transversely narrow protoconid and hypoconid in premolars as a mark of early wear stage of the tooth. Early wear condition of those specimens partly affects the longer occlusal length of cheek teeth tow. The double knots are hipparionid for large and small mandibles and the

ectostylids and protostylids are not visible in middle wear stage.

There are mandibles with the teeth abnormal occlusal morphology: MNHN MAR 89 and MNHN MAR 67.

Size Distribution of Lower Cheek Teeth Row

The size distribution of the lower cheek tooth rows corresponds to that of the upper. The boundary between the larger (*H. prostylum*) and the smaller (*H. moldavicum*) form is 140 to 143 mm in p2-m3 occlusal length (Fig. 12). The anterior and posterior width of the first molar does not sufficiently differentiate teeth rows. The mandible (KNHM A 4846) from Kopran has a cheek teeth row length close to that of *H. moldavicum*.

The mandibles from the Kopran II sub-locality (KNHM RLB 8406, 8407, and 8408) were assigned to the smaller form, *Hipparion ?matthewi* by BERNOR (1985). Although they are small in antero-posterior teeth length of tooth, tooth width is not so. They even belong to the larger group on the m1 width.

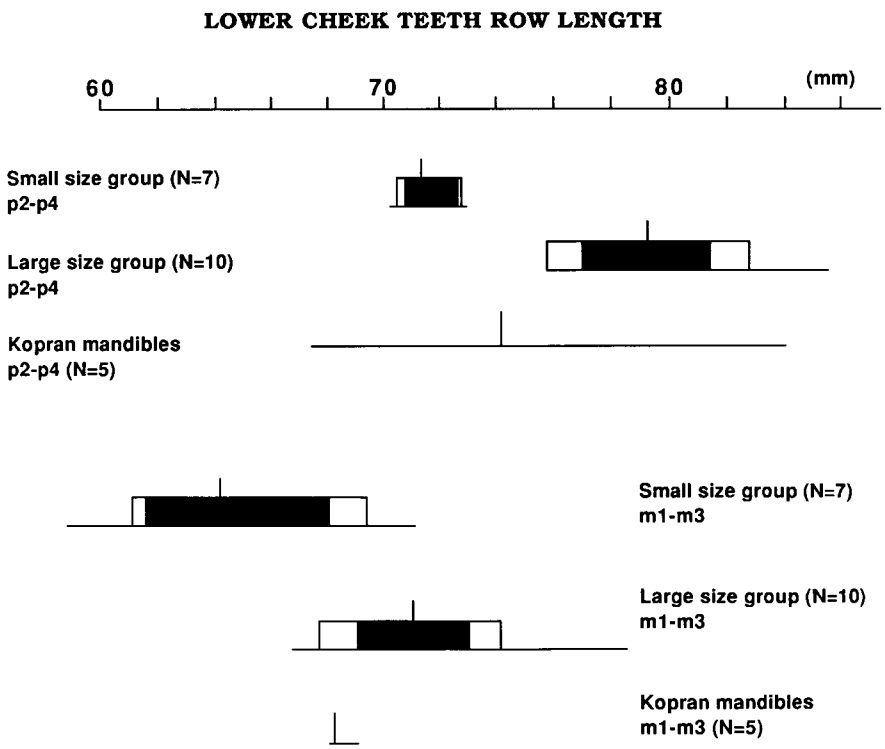

Fig. 12. Dice diagrams on the lower premolar and molar row length. The mandibles were sorted out a priori based on their overall size which had made it possible with some certainty.

The mandibles from Ildtchi and Kopran IV (?) sub-localities belong to the smaller group, and KNHM RLB 8405 from Kopran II also belongs to this group.

Morphology of Lower Premolars

Among the Maragheh mandible specimens there is often a deep ectoflexid in p4, dividing the isthmus into anterior and posterior stems. On the other hand the ectoflexid in p2 is always shallow and that in p3 is very rarely deep enough to separate the isthmus mesiodistally. A deep ectoflexid in p4 occurs in well worn teeth rows, but there is no correspondence with the grouping based on the transverse width of m1, and cheek teeth row length.

Specimens with a deep ectoflexid in p4 compared with m1 are as follows:

KNHM A 4845; W 86501; W 86510; W 86519; W 86521; W 86523; W 8612; W 8621; W 8622; PLB 8405; RLB 8606; MNHN MAR 63; 67; 89; 464; KUAC 95078

The precentage of specimens with a deep ectoflexid in p4 in relation to size clusters based on cheek teeth row length is as follows: the large group=36% (N=7); the small group=29% (N=7); specimens in an early stage of wear were excluded. There is little difference between the two groups. The development of anterior plication on the isthmus

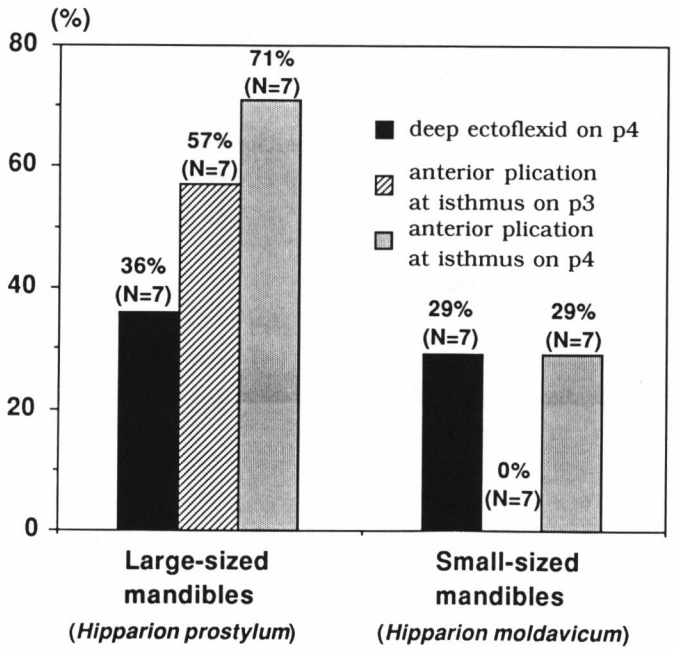

Fig. 13. Percentage of occurrence of some characters on lower cheek teeth in large and small mandibles from Maragheh. Plication on the anterior (mesial) side of the isthmus on premolars shows marked distinction.

of the premolars (p3 and p4) was also counted for both groups: the large group=57% (p3), 71% (p4), N=7; the small group=0% (p3), 29% (p4), N=7; early wear stages were excluded (Fig. 13). The development of anterior plications of the isthmus in p3 and p4 is concordant with the size grouping. However, the number of examined specimens is quite limited (N=7 for both groups).

There is no criterion sufficient for taxonomic discrimination of the Maragheh hipparion mandibles, because it is almost impossible to remove the effect of wear for true size and morphology in the lower cheek teeth. There is no significant difference in occlusal morphology between large and small mandible groups besides the development of anterior plis of the isthmus in premolars. The other specimens of mandible from Maragheh not assigned to size groups due to their incompleteness of tooth buttery have more or less similar occlusal morphology to above mentioned size groups.

Mandibles from Kopran and Kopran II

There are two large mandibles from Kopran: KNHM A 4851 and 4866. Both are young individuals with unworn m3. Their double knots are hipparionid. The anterior plication in the isthmus of p3 and p4 are visible in both specimens. There are four small mandible fragments from Kopran II, KNHM RLB 8405, 8406, 8407, and 8408, among which latter three were assigned by BERNOR (1985) to *Hipparion matthewi* (?). The p2-p4 occlusal length of RLB 8405 (68.1 mm) is comparable with that of KNHM A 4846 from Kopran, belonging to small mandible group. They show deep ectoflexid in p4 and slight mark of anterior plis of the isthmus of p3 and p4 (observed in RLB 8405 and 8406). There is no ectostylid and weak protostylid appears in well worn tooth (RLB 8406). The double knots are hipparionid in all Kopran II specimens. All these specimens might be included in the small mandible group together with A 4846 from Kopran.

Maragheh Deciduous Mandibles

Wien specimens

KNHM W 86502 (Ldp3, dp4; Rdp3, dp4) Kopran: dp3 and dp4 in middle wear stage, m1 erupting in alveolus; KNHM W 86522 (Ldp2-dp4, m1) Ketschawa: dp2-dp4 in middle wear stage, m1 in early wear stage.

Kyoto specimens

KUAC 95032 (L, Rdp2-dp4): early wear stage; KUAC 95028 (Rdp2-dp4 with symphysial region): late wear stage (large ectostylids); KUAC 95038 (Ldp2-m1; Rdp2-m1): dp2-dp4 in late wear stage (large ectostylids in dp3 and dp4). m1 in early wear stage; KUAC 95037 (Ldp2-dp4, m1, m2; Rdp2-dp4, m1, m2): dp2-dp4 in late wear stage (large ectostylids), m1 in early to middle wear stage, tips of metaconid and mesostylid in m2 worn, m3 in anterior part alveolus.

Paris specimens

MNHN MAR 72 (Rdp2-dp4): dp2-dp4 in middle wear stage; MNHN MAR 64 (Lp1, dp2-dp4): p1 unworn, dp2-dp4 in middle wear stage; MNHN MAR 75 (Ldp3, dp4): dp3 and dp4 in late wear stage (large ectostylid in dp3); MNHN MAR 1881 (Ldp2-dp4, m1; Rdp2-dp4, m1): dp2-dp4 in middle wear stage, m1 in alveolus, not worn: MNHN MAR 77 (Ldp2-dp4, m1): dp2-dp4 in middle wear stage, m1 in alveolus, not worn.

In the deciduous tooth rows, the ectostylids are developed in all teeth and the protostylids in dp3 and dp4. Deciduous teeth are elongated mesiodistally compared with the permanent. The metaconids and mesostylids are rounded and linguaflexids are broadened "U" shaped. The hypoconulid of dp4 is expanded distally. There are little differences of the occlusal morphology in deciduous teeth between *Hipparions prostylum, H. urmiense* and *H. moldavicum.*

9. Upper Juvenile Maxillae from Maragheh

Hipparion moldavicum

KUAC 95336: RDP2-DP3, weakly worn (under 1 year for recent *Equus*); MNHN MAR 1795: LP1 and LDP2-DP4 weakly to moderately worn, M1 erupting in alveolus (7 monthes-1 year); KUAC 95335: L&RP1 and DP2-DP4 weakly worn, M1 erupting (7 monthes-1 year); KNHM W 86511: LDP2-DP4 moderately worn, M1 in alveolus unworn (7 monthes-1 year); KNHM RLB 8404: LDP2-DP4 strongly worn, M1 weakly worn (1 year 4 monthes-2 years or more)

Hipparion prostylum

KNHM W 86512: LDP2-DP4 worn (4 monthes-2 year); MNHN MAR 1797: L&RDP2-DP3 very worn (1 year 4 monthes-2 year); MNHN MAR 65: L&RP1, DP2-DP4 moderately worn, LM1 weakly worn (9 monthes-1 year 3 monthes or more); KUAC 95044: LP2, LDP3-DP4, M1-M2, P2 and M1 weakly worn, M2 slightly worn (2–3 years); KUAC 95046: LDP2-DP4 and RDP3-DP4 weakly worn, M1 erupting (under 1 year); KUAC 95332: LDP2-DP4, M1-M2 and RDP3-DP4, M1-M2, M1 weakly worn, M2 erupting (1 year 8 monthes-2 years); KUAC 95326: LDP4, LM1 erupting.

Hipparion incertae sedis

KUAC 95325: RDP2-DP4 moderately worn; KUAC 95327: RDP2-DP4 weakly worn; KUAC 95328: RDP2-DP4 weakly worn.

Dental Morphology of Juvenile Maxillae

There is no difference in the dental morphology between the juvenile maxillae of *H. prostylum* and *H. moldavicum.* General features of the occlusal surface of the deciduous

molars (DP2-DP4) are as follows: irregular-shaped (early wear condition), oval to rounded (advanced wear condition) small protocone; mesiodistally elongated shape of crown; rich enamel plications, especially on posterior wall of the prefossette and anterior wall of the postfossette; double pli caballin; deep hypoconal groove; restricted hypocone; slender anterostyle of DP2.

Facial Morphology of Juvenile Maxillae of *Hipparion moldavicum*

The juvenile skulls of *H. moldavicum* can be distinguished from those of *H. prostylum* by a relatively shorter distance between ventral rim of POF and facial crest. However, this distance increases by the development of the roots of permanent teeth.

In KUAC 95336, the POF is deep medially and dorsoventrally high placed close to the facial crest (FC=17.4 mm). The ventral and posterior rims of the POF are well defined. The posterior pocket is 2.6 mm in depth. The anterior rim is poorly defined and located above the boundary of DP2 and DP3. The posterior rim is probably at a level with the posterior half of DP4. The IOF is located above the anterior half of DP3. The POF is divided into a dorsal and ventral parts by a horizontal ridge in its medial part. The orientation of the long axis of the POF is anteroventral.

KUAC 95335 is a young juvenile individual with the postfossette opened posteriorly into the hypoconal groove. The ventral rim of the POF is well defined and close to the facial crest (FC=15.9 mm). The IOF is at the level of the anterior half of DP3. M1 is erupting.

In MNHN MAR 1795 the ventral part of the POF is deep medially with a well defined rim close to the facial crest (FC=12.2 m). The anterior rim of the POF and the IOF are located above the anterior half of DP3.

KNHM W 86511 (sub-locality is Ildtschi?) has very thin enamel of M2. Its ventral rim is moderately defined and located close to the facial crest (FC=17.5 mm). The IOF is at a level with the DP3 parastyle. The anterior rim of the choanae reaches DP4-M1 boundary.

In KNHM RLB 8404 the ventral part of the POF is close to the facial crest (FC= 15.8 mm) and its rim is moderately defined.

Facial Morphology of Juvenile Maxillae of *Hipparion prostylum*

There are five maxillae in which the facial morphology is observable. However, in most specimens, the dorsal part of the facial region (frontal, nasal, dorsal half of maxilla) is frequently missing.

KUAC 95044 is a young left maxilla fragment with very slightly worn P2, P3 and M1 and M2 in early wear stage. This dental condition is seen in recent *Equus* of 2–3 years. The roots of permanent cheek teeth have almost formed showing high crown. The roots are close to the maxillar bone dorsally. There is no trace of POF.

In KUAC 95046 the first permanent molar (M1) is erupting. The POF is located far from the orbit (POB=32.8 mm) but the distance between ventral rim of POF and the facial crest is small (FC=19.6 mm). This is caused partly by the undeveloped permanent premolars leaving vacant space in the medial part of the maxilla. The infraorbital foramen is at a level with the mid DP3 and the anterior rim of the POF is at a level with the anterior half of DP3. The posterior rim of the POF is located above the posterior half of DP4 and the anterior rim of the orbit above the posterior half of M1. The anterior rim of the choanae reaches DP4 posterior half. A part of the nasal notch is preserved and can be traced to a level with the DP2 parastyle. The long axis of the POF is oriented anteroventrally.

KNHM W 86512 (Ildtschi) has poorly defined ventral rim of the POF which is situated far dorsally above the facial crest (FC=24.8 mm).

In MNHN MAR 1797 the infraorbital foramen (IOF) is located above the posterior half of DP3. The posterior rim of the nasal slit (nasal notch) is placed at the level of the anterostyle of DP2. There is a shallow depression dorsal to IOF, marking the anterior part of the POF.

MNHN MAR 65 has M1 in an early wear stage. The P2 is already formed in the maxillary bone. The infraorbital foramen is located above the mesostyle of DP3. The nasal notch extends to the level of P1. The anterior rim of the POF is at a level with the anterior half of the DP3; it is poorly defined. The ventral part of the POF is preserved and is located far dorsally from the facial crest. A shallow depression is developed in the area between the ventral part of the POF and the facial crest. This is probably postmortem deformation, caused by the vacant space of the maxilla. The orientation of the POF is horizontal; there is no posterior pocket.

KUAC 95332 has no recognizable anterior rim of the POF whose ventral rim is weakly defined and located far from the facial crest. The posterior rim is well defined and located far from the orbit (POB=30.1 mm). There is no posterior pocket. The lacrimal bone does not reach the posterior rim of POF, and the length of the lacrimal bone from the anterior rim of the orbit is 15.3 mm. On the left side a small pit is seen in the posteriormost part of POF. The POF is oriented horizontally. The IOF is at a level with the anterior half of DP4, and the anterior rim of POF with the anterior half of DP3. The anterior rim of the orbit is located above the M2 mesostyle.

KUAC 95326 has wide POB (32.8 mm) and its FC is 28.4 mm. Its facial morphology is similar to those of KUAC 95332 and KUAC 95046.

Differences in the Size of the Deciduous Teeth of Two Facial Morphotypes

The deciduous teeth row length (DP2-DP4) is different in *Hipparion prostylum-urmiense*(?) and *H. moldavicum*. The teeth row (DP2-DP4) occlusal length of the former is, 86.4 mm (KUAC 95332), 92.8 mm (MNHN MAR 65), and 93.8 mm (KUAC 95046).

On the other hand the length of the latter is 81 mm (KUAC 95335).

The available data is limited, but the present materials suggest that the size difference in the skulls of *Hipparion prostylum-urmiense* and *H. moldavicum* are similarly recognizable in their deciduous teeth rows.

***Hipparion* sp. Incertae Sedis**

KNHM W 8623 (Ketschawa) orbital region with LM2-M3 and RM3; KNHM W 86524 (Ketschawa), snout region with maxilla, premaxilla, and nasal; KUAC 95323 (−20 m) anterior part of maxilla, premaxilla, and nasal, with buccinator fossa.

KNHM W 8623 preserves orbital region but no POF. The width of POB is unknown. KNHM W 86524 shows deep nasal notch incised with the level of the mid of P2. The dorsal rim of the premaxilla of KNHM W 86524 is straight and the nasal notch extracts deeply, differing from those of MNHN MAR 359-1475 belonging to *H. prostylum* and MNHN RLB 8003 (*H. moldavicum*). The morphology of this specimen (W86524) is similar to that of *Hipparion urmiense* (MMTT 13/1342).

10. Upper Snout

Canine Size as Sexual Dimorphic Character

EISENMANN et al. (1987) and MACFADDEN (1987) discussed the usefulness of canine size for discriminating female and male individual of hipparions. Referring to GROMOVA (1952), EISENMANN et al. (1987) maintained that canine size as a criterion of sex is not established.

It is difficult to distinguish the sex in the case of hipparion. Overall size, facial morphology, dental characters and proportions of the limbs do not reflect the difference of sex in contrast to Artiodactyla. No character, except canine size, has been considered useful for assessing sex of hipparions. At present it is probable that canine size is the most useful character for sex determination. Difference between female and male specimens in upper canine size is equivalent to that of the lower.

The boundary between female and male is at about 7 mm in anteroposterior diameter of the canines for medium to large-sized hipparions (not applicable to very large-sized hipparions such as large *Hipparion* from Samos). The anteroposterior diameter of the upper canine of the females ranges from 4 to 6.5 mm in medium to large-sized hipparions (the specimens are from Eurasian and African Late Miocene localities). In transverse diameter of the canine the boundary between females and males is at about 5 mm for medium to large-sized hipparions. The transverse diameter of the upper canine of females ranges from 2 to 4.5 mm (choice of specimens is the same as for the upper). These two diameters were measured in alveolus so that alveolus hole size could be measured if the teeth had been lost.

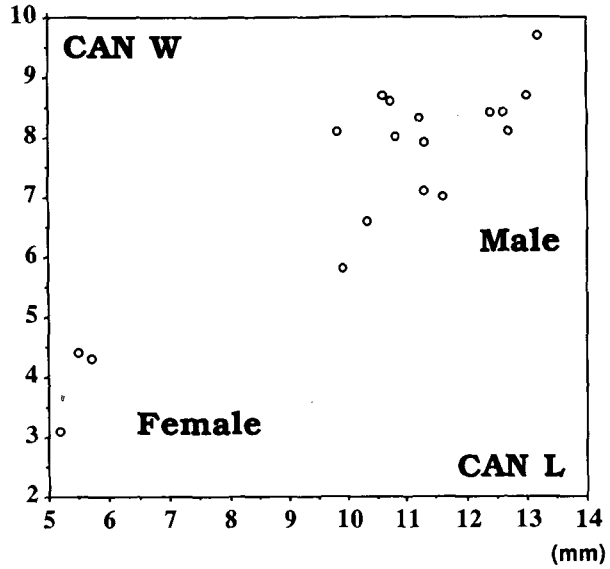

Fig. 14. Transverse width of upper canine plotted against the mesiodistal width in Maragheh *Hipparion*. Smaller canines are of female individuals and larger of male.

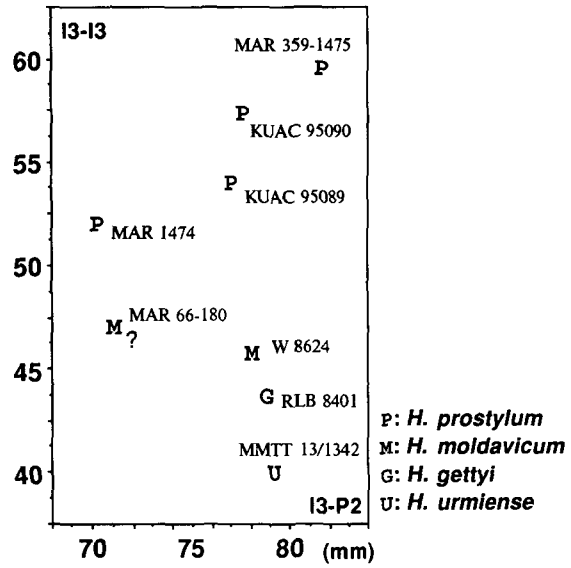

Fig. 15. Width across both I3 plotted against the diastemata length between I3 and P2 in upper snout. *H. prostylum* from Maragheh has robuster proportion of snout than other taxa.

The snouts from Maragheh are heterogeneous in their canine size and they are divided into two clusters (Fig. 14).

Examples of heterogeneity of canine size observed in some local samples are as follows:

Example 1: *Hipparion prostylum* from Saloniki (Greece) are well analyzed for their canine size. The anteroposterior and transverse diameters of the canine of MNHN SLQ 84b, estimated as female, are 6.3 and 4.2 mm, respectively. Those of SLQ 74, a male, are 10.9 and 9.9 mm, respectively.

Example 2: *H. africanum* from Bou Hanifia (Algeria), Vallesian of North Africa, is also well resolved what comes to sex by its canine size. The anteroposterior and transverse diameters of the canine of MNHN 1951-9-125, female, are 6.2 and 4.3 mm, respectively. Those of MNHN 1951-9-116, a male, are 14.0 and 8.6 mm. In MNHN 1951-9-141, they are 14.0 and 9.3 mm, indicating male sex.

Length and Width of the Snout and Sexual Dimorphism

No sexual dimorphism was observed in the width across canines, diastemata length (I3-P2), snout length (prosthion-midpoint of both P2) and skull size (P2-Orbit) of *H. africanum* from Bou Hanifia and of *H. prostylum* from Saloniki. The difference in snout proportions can be considered taxonomic, though the individual variation exists.

Sorting of Upper Snouts from Maragheh

Three clusters of upper snout from Maragheh can be distinguished on the basis of their proportions (Fig. 15). These clusters show a good correspondence to grouping of lower snout.

1) The robust upper snouts with transversely straight incisor arrangement are of *Hipparion prostylum*. Proportions similar to these are shown by the Saloniki *H. prostylum*, the same species from Mt. Luberon, and *H. schlosseri-dietrichi* from Samos. MNHN MAR 1474, MAR 359-1475, KUAC 95089 and 95090 show that they belong to *H. prostylum* on their facial morphology. MNHN MAR 70 and KNHM W 86516 from Zad Baschi have wide snout. KNHM W 8615 from Kopran II has also wide snout.

2) The snouts with intermediate proportions are represented by the skulls of *Hipparion gettyi* from Kopran (KNHM RLB 8401) and by KNHM W 8624 (old female) from Dschingirdera.

As there is no specimen of *Hipparion moldavicum* with the snout region intact from Maragheh, the snout proportions of that taxon are not known. But the proportions of Pikermi *Hipparion mediterraneum*, with similar facial morphology to the Maragheh *moldavicum* form and to type *H. moldavicum* from Taraklia, are more slender than that of *H. prostylum* and comparable with the intermediate snouts from Maragheh.

MNHN MAR 66-1800 (male adult) with cheek teeth rows and snout region clearly

exhibits the curved arrangement of incisors and small overall size, but its proportions are similar to that of *H. prostylum*. KNHM W 8624 from Dschingirdera, old female, has curved incisors' arrangement.

3) MMTT 13/1342, a female individual with small canines, has a very slender (narrow) upper snout. MNHN MAR 90 is an isolated upper snout showing the proportions similar to that of MMTT 13/1342.

The lower snout, corresponding to the above three upper snout forms, are recognized.

Upper Snout Proportions of Some Late Miocene Eurasian Hipparions

There are differences in snout proportions among Eurasian late Miocene hipparions, associated with taxonomic diversity.

Vallesian and large Turolian hipparions such as *H. primigenium, H. africanum,* and large hipparion of Samos have medium snout proportions and large overall size. Large Turolian hipparion in U.S.S.R. region, *H. garedzicum* from Udabno, Gruzia S.S.R. and *H. giganteum* from Grebeniki, Ukraina S.S.R. have also medium snout proportions.

Turolian *Hipparion prostylum* from Mt. Luberon and Saloniki, and *H. schlosseri-dietrichi* from Samos exhibit robust proportions of the snout with short snout length and large snout width. Turolian "*Hipparion mediterraneum*" group with a triangular POF close to the orbit, has medium snout proportions. These forms are represented by *H. mediterraneum* from Pikermi of Greece, *H. moldavicum* from Taraklia of Moldavia S.S.R. *Hipparion prostylum* and *H. schlosseri-dietrichi* with short snout have long POB relative to their skull size, compared with *H. mediterraneum* and *H. moldavicum.*

Small hipparion, *H. matthewi* from Samos (KNHM V 131 and A 4742) has snout proportions similar to or robuster than *H. mediterraneum,* however, its overall size is small.

Sorting out of Lower Snout

The lower snouts from Maragheh were sorted out by using absolute size of muzzle width (across canines, and/or third incisors), its relative size to diastemata length (i3-p2), and mode of the incisor arrangement (Fig. 16).

The upper snouts of *Hipparion prostylum* from Saloniki and Mt. Luberon show a flat and straight outline of incisor (i1-i3) arrangement. This straight arrangement in the snout region is also caused by old age (strong wear). Individuals over 8 years of recent *Equus* exhibit a straight outline (HABERMEHL, 1975).

Three groups of lower snouts were distinguished as in the upper snouts, namely: robust, moderate, and very slender. These three divisions could correspond to those of the upper snout based on the same variables.

1) Robust lower snouts belong to the wide upper snouts of *Hipparion prostylum* of Maragheh. KNHM A 4846 (female) from Kopran has wide snout and straight incisors arrangement with large overall size. The cheek teeth row size of the specimen is medium

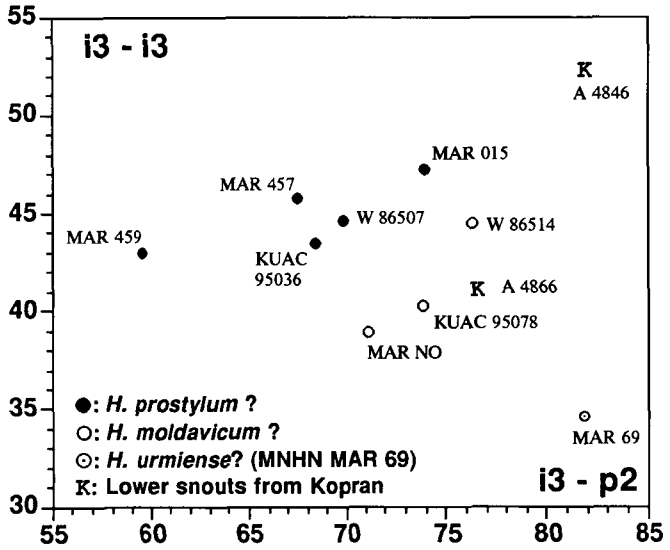

Fig. 16. Width across both i3 plotted against the diastemata length between i3 and p2 in lower snout. Similar pattern of difference in proportion can be recognized to that in upper snout.

(P2-M3 length is 137.9 and 135.4 mm). KNHM W 8616 from Ketschawa, W 8617 from Ketschawa, W 8618 from Kara Kend, and MNHN MAR 015 are all male and show wide snout and straight arrangement of incisors. KUAC 95036 (male), MNHN MAR 457 (adult female) and KNHM W 86507 (male) from Ildtschi have robust snouts. MNHN MAR 459 is small in size but robust in proportions.

2) Slender lower snout can be associated with the upper snout of *H. moldavicum*. MAR 017 (male) and KUAC 95078 (female) exhibit narrow snouts. KNHM A 4866 from Kopran is a very young individual with p2-m2 in early wear stage and unworn m3 and canines in alveolus, having narrow snout. KNHM W 86514 from Ketsuchawa, old male, has slender snout. KNHM A 4867 (male) from Ketschawa has cuved incisor arrangement, though it has intermediate between the robust and slender lower snouts.

3) Very slender lower snouts might correspond to *Hipparion urmiense* (=*H. campbelli*) in Maragheh. KNHM W 8620 from Kopran II is a very old male with triangular outline of an incisor. MNHN MAR 69 is an adult male with very narrow snout. This specimen may correspond to the upper snout with very narrow width (e.g. MNHN MAR 90).

Correspondence between Upper and Lower Snouts

The upper and lower snouts from single localitiy with monotypic or clearly discriminated taxonomic units were selected to establish the association between upper and lower snout size. Examined materials are those of *Hipparion africanum* from Bou Hanifia,

Vallesian of North Africa, and of *H. prostylum* from Saloniki, Turolian of Greece; and hipparions from Turolian localities in North China (Loc. 30 and 44, the Shanxi province, stored in the Uppsala University). The measured variables are distance between I/i3-P/p2 distance (diastemata length) and width across posterior edges of canines in alveolus. These values and proportions of the upper and lower snouts were compared for the specimens which belong to a single taxonomic group.

The result of the comparison indicates that there are not large differences between upper and lower diastemata length, or width across canines. The width of the lower snout is slightly smaller than that of the upper one (roughly estimated as the lower is smaller than the upper at 88%). Therefore, if the measurements for either the upper or the lower snout could be obtained, it would be possible to estimate that of the other. KNHM A 4867 from Ketschawa is an occluded male upper and lower snouts in an adult age. They both show curved arrangement of incisors and narrow width of I3-I3.

11. Correspondence between Cranial and Postcranial Elements

The stratigraphic occurrences of each skull morphotypes in the Maragheh Foramtion are distinct. *H. gettyi* comes from only the lower part of the sequence, and *H. urmiense* from the upper part. *H. prostylum* and *H. moldavicum* are abundant from the middle to upper parts (Table 1).

Table 1. Stratigraphic occurrences of skull morphotypes in the Maragheh Formation.

Horizons (m)	Sub-localities	morphotypes	
+7	UC 26	*urmiense*	
+4	UC 39		
-18	UC 13/; Ildtschi		
-20	Kyoto	*prostylum*	*moldavicum*
-28	UC 7, 14		
-30	UC 20		
-28~-52	Kara Kend·	*prostylum*	
-28~-52	MNHN	*prostylum*	*moldavicum*
-30~-52	Ketschawa	*prostylum*	*moldavicum*
-115	Kopran II; UC 41, 44		
-115~-150	Kopran; UC 43, 9, 48		*gettyi*

Here, we suggest a hypothesis on the association of the cranial and the postcranial morphotypes of the Maragheh hipparions, based on the stratigraphic occurrences and size of them, and on the information in other localities.

1) *Hipparion gettyi* from the lower part of the Maragheh Formation has medium sized metapodials and tarsal elements. The skull of this form is characterized by a slender to middle upper and lower snouts, and by medium-sized cheek tooth row length.

2) *Hipparion moldavicum* from the middle to upper parts of the formation, has small

and slender metapodials and small tarsal elements. The mandibles and the lower and upper cheek teeth of this form are of medium size. The snout is medium to slender in proportions.

The small hipparion assigned to *Hipparion* cf. *matthewi* by BERNOR (1985) may be included in this form.

3) *Hipparion prostylum* from the middle to upper parts of the formation, has large and probably robust metapodials and large tarsal elements. The mandibles and the lower and upper cheek teeth of this form are characterized by large size. The plication of the lower cheek teeth is developed in this form. The snout is robust (wide).

4) *Hipparion urmiense* (=*H. campbelli* BERNOR) from the upper parts of the formation, has large and robust metapodials and large-sized tarsal elements. The mandibles and lower and upper cheek teeth of this form are of large size. The snout is very slender in MMTT 13/1342.

An alternative hypothesis on the association that could not be rejected is:

5) The large and slender metapodials associated with the medium sized tarsal elements correspond to *Hipparion urmiense* (*H. campbelli* BERNOR) and/or even to *Hipparion prostylum*.

If accepted this hypothesis, the MC III of *H. urmiense* shows a smaller angle between the facets for the magnum and hamatum than the other two groups: the small and slender, and the robust.

The combination of skull of *H. urmiense* and large and slender metapodials is partly supported by the example of other hipparions with reduced POF, such as *Hipparion hippidiodus* from Gansu, northern China and *H. platygenys* from Taraklia, Moldavia S.S.R. having large postcranial bones. On the basis of data by QIU et al. (1987) and our personal observation, *Hipparion hippidiodus* with a reduced POF and slender snout region (M 3818 from Loc. 43, Qingyang) has third metapodials similar to those of *H. mediterraneum* from Pikermi, Greece, in proportions.

The hypotheses 4) and 5) are equally plausible and it is impossible to determine which one is more reasonable than the other at present.

12. General Discussion

The hipparion assemblage at Maragheh shows a close relationship with those of the localities on the northern shore of the Black Sea. *Hipparion moldavicum* from Maragheh is closely related to *Hipparion mediterraneum* from Pikermi, Greece. The eastern extension of the distribution of these forms is represented by *Hipparion fossatum* (=*H. forstenae* by QIU et al., 1987) in northwestern Shanxi of northern China. *Hipparion urmiense* with a reduced POF from Maragheh suggests a phylogenetic relationship with *Hipparion platygenys* from Taraklia in the northern Black Sea region and *Hipparion hippidiodus* from Qingyang in the

Gansu province of northern China. *Hipparion prostylum* from Maragheh has snout and facial characters similar to those of the taxon from Mt. Luberon and Saloniki, and of *H. schlosseri-dietrichi* from Samos. *Hipparion gettyi* discovered from the lower part of the Maragheh Formation is possible sister group of the "*Hipparion mediterraneum*" group.

There are Turolian mammalian localities in Eurasia where more than three hipparions have been discovered. Samos Q1 of Greece yields up to four hipparion forms. These are *Hipparion* sp. medium sized with a double fossa; *H. schlosseri-dietrichi*; *H. proboscideum*; and *Hipparion* sp. large form (FORSTÉN, 1980b; KOUFOS and MELENTIS, 1984). In Saloniki, there are three forms: *Hipparion prostylum*, *H.* cf. *mediterraneum*, and *H. matthewi* (WOODBURNE and BERNOR, 1980). In Maragheh, at least three hipparions co-exist in the upper horizon (−18 : −20 m below the "Loose Chips" pumice bed), such as: *Hipparion moldavicum*, *H. prostylum*, and *H. urmiense*.

The localities which yield two hipparion forms, a large and a small, are widely distributed in Eurasia, e.g., Pikermi (Greece); Taraklia (Moldavia S.S.R.) and Grebeniki (Ukraina S.S.R.); Garkin and Kayadibi (Turkey); Pavlodar (Kazakhstan); Baode (Loc. 30), Shanxi province and Qingyang (Loc. 115 and 116), Gansu province in northern China. The difference in the limb proportions observed in above mentioned localities could be phylogenetic. The large-sized hipparionine taxa, in general, would have robust limbs and the small-sized taxa slender ones.

The change in limb proportions within a single evolutionary lineage (monophyletic group), conventionally recognized in the third metapodial, is an interesting subject. *Hipparion mediterraneum* from Pikermi, Greece, and *H. moldavicum* from the northern shore of the Black Sea and Maragheh have slender-proportioned (elegant) MC III and MT III. The limb proportions of *Hipparion proboscideum* with large skull from Samos, which is considered phylogenetically associated to the "*H. mediterraneum*" group (WOODBURNE and BERNOR, 1980), have not yet been clarified.

Hipparion prostylum from Maragheh has a larger skull than *H. moldavicum* from the same locality, and is supposed to have robust third metapodials. However, the skulls of *H. prostylum* from Mt. Luberon and Saloniki co-occurred with slender metapodials (FORSTÉN, 1983; and my personal observation). It is possible that *H. prostylum* of large size has large but slender metapodials which are expressed in the Maragheh specimens.

The hipparions discriminated on limb proportions and cranial morphology can not be differentiated on dental morphology. The hipparion species which co-occurred in a single locality were not dietary differentiated.

Hipparion prostylum from Mt. Luberon, Saloniki, and Maragheh, and *H. schlosseri-dietrichi* from Samos have reduced POF situated dorsally and far from the orbit, and also have robust upper and lower (?) snouts. A robust snout is a synapomorphy of *H. prostylum* and *H. schlosseri-dietrichi*. On the other hand, the very slender proportions of snout is also derived character in Eurasian hipparions. The intermediate or moderate

proportions of snout seen in *H. mediterraneum-moldavicum* group and large hipparions of Vallesian and Turolian ages, though varying in size, is plesiomorphic.

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Measurements on skull (upper jaw)

I3-P2: Distance between the posterior distal edge of I3 and mesial edge of P2.
NN-P2: From posterior edge of the nasal notch to mesial edge of P2 at alveolus.
NN-IOF: From posterior edge of the nasal notch to posterior edge of the infraorbital foramen.
NN-POF: From posterior edge of the nasal notch to posterior rim of the preorbital fossa.
NN-ORBIT: From posterior edge of the nasal notch to anterior rim of the orbit.
P2/HEIGHT: Height in front of P2.
PROST-NSL: From Prosthion to the posterior edge of the nasal notch (the back of the narial opening).
APL/POF: Anteroposterior diameter of the preorbital fossa.
DVH/POF: Dorsoventral height of the preorbital fossa.
IOF-POF: From the posterior edge of the infraorbital foramen to the posterior rim of the preorbital fossa.
POB: Preorbital bar width, from the posterior rim of the preorbital fossa to the anterior rim of the orbit.
ORB/D: Horizontal diameter of the orbit.
P2-ORBIT: From the anterior edge of P2 at the alveolus to the anterior rim of the orbit.
SNOUT/L: From Prosthion (point situated between the base of the I1) to the middle of the line connecting the anterior borders of P2.
PALATE/L: Minimal length between the middle of the line connecting the anterior borders of the P2 and the point situated at the base of the palatal spur.
VOMER L: From the anterior edge of the choanae to the middle of the vomerine notch.
BASCR L: From the middle of the vomerine notch to Basion.
MUZZLE/W: Width at the posterior edges of both canines.
ANTPOF ALV: From the anterior most point of POF to the alveolar level, vertical to the palatal plane.
POSTPOF ALV: From the posterior most point of POF to the alveolar level, vertical to the palatal plane.
VENT POF ALV: From ventral rim of POF to the alveolar level, vertical to the palatal plane.
FC: From ventral rim of POF to the edge of the facial crest, vertical to the palatal plane.
IOF-ALV: From the posterior most point of the IOF to the alveolar level, vertical to the palatal plane.
CL: Mesiodistal diameter of upper canine at the alveolar level.
CW: Lateromedial diameter of upper canine at the alveolar level.
M1W: Palatal width at the level of P4-M1 boundary at the alveolus.
ANT POF: Position in the cheek teeth row above which the anterior rim of POF is located. ANTERO=Anterostyle; PARA=Parastyle; MESO=Mesostyle; META=Metastyle; ANT=Anterior half of tooth; POST=Posterior half of tooth; -=Boundary of two teeth.
POST POF: Position in the cheek teeth row above which the posterior rim of POF is located.
ORBIT: Position in the cheek teeth row above which the anterior rim of the orbit is located.
NASAL: Position in the cheek teeth row above which the posterior edge of the nasal notch is located.
CHOANAE: Position in the cheek tooth row on which the most anterior point of the choanae is located.
IOF: Position in the cheek teeth row above which the posterior edge of the infraobital foramen is located.
LACRIMAL: The lacrimal bone touch (YES) or not touch or invade (NO) the posterior part of POF.
POSK (Depth): Development of the posterior pocket and depth.
ANT DEF: Definition of anterior rim of POF, 0=no rim; 1=weakly defined; 2=clearly defined.
VENT DEF: Definition of ventral rim of POF, 0=no rim; 1=weakly defined; 2=clearly defined.
AXIS POF: Orientation of longer axis of POF, AV=anteroventral direction; HZ=horizontal direction.
SUBNASAL: Development of the subnasal fossa.
AGE: Ontogenetic age assessed by dental wear. Juvenile means the deciduous teeth are in function.
SEX: Sex determined by size of the upper canines.
SUB-LOC: Sub-locality. Kyoto=site by Kyoto University (−20 m below the 'Loose Chips' Marker bed).
TAXON: Taxonomic assignment based on the facial morphology and size.
(B): From the most lateral points of the zygomatic arch to the middle of the supra-occipital crest.
PROSTHION-ORBIT/ANT (A): From the Prosthion to the anterior rim of the orbit.
ORBIT-PROSTHION (23): Anterior ocular line, from the Prosthion to the most lateral point of the orbital process.
BAIO-CHOA (5): From the anterior most edge of the choanae to the Basion.

RROST.-BASION (6): Basilar length from the Prosthion to the Basion.
TEMPORAL CAV. L (16): Maximum length of the temporal fossa.
BASION-ETHM (17): Distance between the basion and the foramen ethmoidalis.
FRONT (18): Greatest width between the orbital process.
JUGAL WIDTH (19): Greatest width between the exterior most point of the orbital process.
CHOANAE L (10): Choanae length in projection from the anterior most edge of the choanae to the point of meeting of the guttural and caudal parts of the Vomer.
ANT. WIDTH CHOANAE (12): Maximum width of the choanae.

Measurements on upper cheek teeth

All are measured on the occlusal surface.
APL: Anteroposterior length of tooth.
TRNW: Transverse width of tooth.
PRTL: Anteroposterior length of protocone.
P2-P4: Length of premolar row.
M1-M3: Length of molar row.
P2-M3: Length of cheek tooth row.
PCB: Number of the Pli caballin on six cheek teeth. Left end is P2 and right end M3.
PCL: Plication counts on M1. If other tooth, indicated by ( ).
CL: Mesiodistal diameter of upper canine at the alveolar level.
CW: Lateromedial diameter of upper canine at the alveolar level.
AGE: Ontogenetic age assessed by the teeth wear.
SEX: Sex determined by the canine size.
SUB-LOC: Sub-locality.
TAXA: Taxonomic assignment based on the facial morphology and size.

Measurements on mandible and lower cheek teeth

All measurements on the occlusal surface.
apl: Anteroposterior length of tooth.
amcw: Transverse width at the metaconid-protoconid.
petw: Transverse width at the mesostylid-hypoconid.
mcms: Anteroposterior length of the double knots.
P2-P4: Length of premolar row.
m1-m3: Length of molar row.
p2-m3: Length of cheek tooth row.
prtsd: Development of the protosylids on teeth. Left end is p2 and right m3.
CL: Mesiodistal diameter of lower canine at the alveolar level.
CW: Lateromedial diameter of lower canine at the alveolar level.
i3-p2: Distance between the distal edge of i3 and anterior edge of p2 at the alveolus, if snout region preserved.
muzzle width: Width between the posterior alveolar edges of both i3.
p2h: Height of the mandible in front of p2, vertical to ventral rim of the body.
m1h: Height of the mandible in front of m1, vertical to ventral rim of the body.
double knots: Type of the double knots. HIPP=Hipparionid; CAB=Caballoid; -=intermediate condition.
AGE: Ontogenetic age assessed by teeth wear.
SEX: Sex determined by the canine size.
SNOUT: Preservation of the lower snout part
SUB-LOC: Sub-locality.

Appendix 1 Measurements of Skull.

SPECIMENS	KUAC 95333	KUAC 95330	KUAC 95089	KUAC 95331	KUAC 95329	KUAC 95090	KUAC 95336
I3-P2			77.5			78	
NN-P2						63.7	
NN-IOF						75.3	
NN-POF (31)						103.8	
NN-ORBIT						137.7	
P2/HEIGHT (25)			76.5			76.8	
PROST-NSL (30)			120			120.6	
APL/POF (33)		65.3	56.9	53	59.5	52.3	48.5
DVH/POF (35)		48.7	26.8	29.3	41.6	29.6	28.7
IOF-POF (34)		70	53.2	40.2	56.9	36.3	39.6
POB (32)		26.4	37.7	39.4	27.3	34.2	
ORB/D (28)		45.7			53.4	55.8	
P2-ORBIT			159	150.7	146.3	150	
SNOUT/L (1)			104.9			94.3	
PALATE/L (2)	118		99.8			109	
VOMER L (3)			102.8			92	
BASCR L (4)						85	
MUZZLE/W			47.4			44.2	
ANTPOF ALV		52	67.1		56.6	60.2	
POSTPOF ALV (38)		66	76	73.3	71.9	72.5	
VENT POF ALV	48.1	36.8	53.3	57.3	42.7	49.9	29.6
FC (36)	33.1	23.5	31.3	39	25.4	35.1	17.4
IOF-ALV		39.2	52.4	53.7	49.5	54.7	35.1
CL			0			11.3	
CW			0			7.9	
M1W		58.7	67.8	55.7+	46.5	61.5	
ANT POF		P4 PARA?	P4 PARA			P4ANT	DP2-DP3
POST POF		M3 PARA	M2 ANT	M2PARA	M3 PARA	M2 MESO	DP4 POST
ORBIT		M3+	M3 MESO	M3 MESO	M3+	M3 META	
NASAL			P2 ANTERO			P2ANTERO	
CHOANAE	M2-M3	M2 ANT	M1-M2	M2 ANT	M2 ANT	M2 ANT	
IOF	P4 ANT	P3 META	P4 ANT	P4 MESO	P4 ANT	P4-M1	DP3 ANT
LACRIMAL		YES	NO	NO	YES	NO	YES
POSK (Depth)		YES (4.4)	YES (?)	YES (5.3)	YES (3.9)	NO	YES (2.6)
ANT DEF*			0			0	2
VENT DEF*		2	1	1	2	1	2
AXIS POF		AV	HZ	HZ	AV	HZ	AV
SUBNASAL			NO	NO	NO	NO	NO
AGE	Adult	Adult	Young	Young	Adult	Adult	Juvenile
SEX	?	?	Female	?	?	Male	?
SUB-LOC.	Kyoto	Kyoto	Kyoto	Kyoto	Kyoto	Kyoto	Kyoto
TAXON	Prost.	Mold.	Prost.	Prost.	Mold.	Prost.	Mold?
		@130(B)	40.1 (12)	33.2 (12)	31.9 (12)	258(A)	
		39.6(12)	61.2(10)			310(23)	
			74.7(16)			83.9(5)	
						38.6(6)	
						63.5(16)	
						152((17)	
						152.6(18)	
						150(19)	
						60.5(10)	
						25.7(12)	

Appendix 1 (continued)

SPECIMENS	KUAC 95335	KUAC 95332	KUAC 95046	KUAC 95045	MAR 1477	MAR 469	MAR 466
I3-P2							
NN-P2							63.5
NN-IOF							72.7
NN-POF (31)							108.6
NN-ORBIT							140
P2/HEIGHT (25)							
PROST-NSL (30)							
APL/POF (33)		56.5	53.2		78.9	67	74
DVH/POF (35)			32		55.8		45.3
IOF-POF (34)		33.6	36.4		66.4	52	42
POB (32)		30.1	32.8		28.5	27.7	29.8
ORB/D (28)					59.3		48
P2-ORBIT		136.2	122.8		150	160	153
SNOUT/L (1)							
PALATE/L (2)							98
VOMER L (3)							
BASCR L (4)							
MUZZLE/W							
ANTPOF ALV		58.2	44.9		59.8	56	51.2
POSTPOF ALV (38)		75.7	58.5		73.7	71.2	75.2
VENT POF ALV	28.2	53.7	30.7	55.6	39.2	45	47.7
FC (36)	15.9	32.9	19.6	32	23.5	24.4	24.2
IOF-ALV	37.5	56.2	36.7	59.4			
CL							
CW							
M1W	51.2				55	62.8	56
ANT POF		DP3ANT	DP3 PARA		P3 POST	P4 PARA	P3 POST
POST POF		M1ANT	DP4 POST		M3 PARA	M3 MESO	M3 PARA
ORBIT		M2 MESO	M1 POST		M3+	M3+	M3+
NASAL			DP2 PARA?				P2 ANT
CHOANAE	DP4 ANT	M1 MESO	DP4 POST	M1 POST	M1-M2	M2 ANT	M2 ANT
IOF	DP3 ANT	DP4 PARA	DP3 MESO	DP3 POST	P4 PARA	P4 MESO	M1 PARA
LACRIMAL		NO	NO	NO	NO	YES	YES
POSK (Depth)		NO	NO		YES (6.3)	YES (7.6)	YES (2.6)
ANT DEF*		0	1		2	2	2
VENT DEF*	2	1	1	2	2	1	2
AXIS POF		HZ	HZ		AV	AV	AV
SUBNASAL			NO		NO	YES?	YES?
AGE	Juvenile	Juvenile	Juvenile	Juvenile	Adult	Adult	Adult
SEX	?	?	?	?	?	?	?
SUB-LOC.	Kyoto	Kyoto	Kyoto	Kyoto	Paris	Paris	Paris
TAXON	*Mold?*	*Prost.*	*Prost.*	*Prost.*	?	*Mold.*	*Mold.*
			32.5 (12)				

Appendix 1 (continued)

SPECIMENS	MAR 71	MAR 359 /1475	MAR 62	MAR 1476	MAR 1474	MAR 465	MAR 1804
I3-P2		81.6			70.2		
NN-P2		66	64.6		67.4	61.8	
NN-IOF		77.7	55.6	54	65.3	68.2	
NN-POF (31)		113.5	115.7	103.2	100	106.6	
NN-ORBIT		151.5	139	128	136.8		
P2/HEIGHT (25)			81.3		68		
PROST-NSL (30)					114.7		
APL/POF (33)	50	62.3	79.1	70.5	69.5	55.5	
DVH/POF (35)	33.5	33.8	48.5	50.4	28.5	34.7	
IOF-POF (34)	48	45.9	69.8	62.1	41.9	46	
POB (32)	39	42	23.9	25.4	38	@35	
ORB/D (28)			54.5	51.4			
P2-ORBIT	160	161	144.8	150	151	@149	
SNOUT/L (1)		100+			94		
PALATE/L (2)		112.6	95.8		98.8		
VOMER L (3)							
BASCR L (4)							
MUZZLE/W		48.3			44.3		
ANTPOF ALV	57.2	63.2	54.3	56.5	54	65.1	
POSTPOF ALV (38)	70.5	81.2	71.2	69.2	76.9	78.4	
VENT POF ALV	56.2	54	39.4	37	55.6	56.6	47.6
FC (36)	44.3	34.6	19.9	23.3	38.3	34.1	30.6
IOF-ALV							
CL		11.2			10.6		
CW		8.3			8.7		
M1W	59.6	68			43		
ANT POF	P4 MESO	P4 PARA	P3 ANT	P4 PARA	P3 MESO	P4 PARA	
POST POF	M2 MESO	M2 META	M3 PARA	M3 ANT	M2 POST	M3 PARA	
ORBIT	M3+	M3+	M3+	M3+	M3+	M3+?	
NASAL		P2 PARA	P2 PARA	P2 ANTERO	P2 PARA-	P2-	
CHOANAE	M2 PARA?	M2 MESO	M2 ANT	M2 MESO	M2 MESO		
IOF	P4 POST	P3 MESO	P3 MESO	P4 ANT	P4 MESO	P4 MESO	P4 MESO
LACRIMAL	NO	NO	YES	YES			
POSK (Depth)	NO	YES (2.2)	YES (4.1)	YES (2.6)	NO	NO	
ANT DEF*	0	0	2	2	0	0	
VENT DEF*	1	2	2	2	1	1	
AXIS POF	HZ	HZ	AV	AV	HZ	HZ	
SUBNASAL	NO	NO	NO	YES?	NO	NO	
AGE	Adult	Adult	Adult	Adult	Old	Old	Old
SEX	?	Male	?	?	Male	?	?
SUB-LOC.	Paris	Paris	Paris	Paris	Paris	Paris	Paris
TAXON	Prost.	Prost. 176(18)	Mold.	Mold.	Prost. 236(A)	Prost.	?

Appendix 1 (continued)

SPECIMENS	MAR 66/1800	MAR 1797	MAR 1796	MAR 65	MAR 1795	MAR 70	MAR 90
I3-P2	71						
NN-P2		62.7		50.8			
NN-IOF		45.7		58.3			
NN-POF (31)				87			
NN-ORBIT							
P2/HEIGHT (25)							
PROST-NSL (30)							
APL/POF (33)				42.2			
DVH/POF (35)				23			
IOF-POF (34)				32			
POB (32)							
ORB/D (28)							
P2-ORBIT				130+			
SNOUT/L (1)							
PALATE/L (2)				108+			
VOMER L (3)							
BASCR L (4)							
MUZZLE/W	41.2			43.8		49.2	33
ANTPOF ALV		50.8		58.7			
POSTPOF ALV (38)				@62			
VENT POF ALV			40.5	51.4	29.5		
FC (36)				31.7	12.2		
IOF-ALV							
CL	11.3						
CW	7.1						
M1W				58			
ANT POF		DP2-DP3		DP3 ANT	DP3 PARA		
POST POF							
ORBIT							
NASAL		DP2 MESO		DP2-			
CHOANAE				M1 MESO+			
IOF		DP3 MESO		DP3 MESO	DP3 PARA		
LACRIMAL							
POSK (Depth)				NO			
ANT DEF*		1		1			
VENT DEF*				1			
AXIS POF				HZ			
SUBNASAL		YES?		NO			
AGE	Adult	Juvenile	Juvenile	Juvenile	Juvenile	Adult	Adult
SEX	Male	?	?	?	?	Male	Male
SUB-LOC.	Paris	Paris	Paris	Paris	Paris	Paris	Paris
TAXON	Mold?	Mold?	Prost?	Prost.	?	?	?

Appendix 1 (continued)

SPECIMENS	RLB 8003	A 4848	W 86525	A 4844	W 8615	RLB 8401	A 4847
I3-P2						78.8	
NN-P2	59.1					72.9	68
NN-IOF	57.6					49.2	55
NN-POF (31)	99.1					90.3	106.5
NN-ORBIT	122.3					136	143
P2/HEIGHT (25)						90.6	70
PROST-NSL (30)						137	
APL/POF (33)	62.3					59.6	56
DVH/POF (35)	44.4					32.5	35.3
IOF-POF (34)	49.3					65.3	64.2
POB (32)	23.1	32.7	27			45	36
ORB/D (28)	56					52.6	56.4
P2-ORBIT	137					152.3	161
SNOUT/L (1)				108.7		100.8	
PALATE/L (2)						115	103
VOMER L (3)							
BASCR L (4)							
MUZZLE/W					49.6	38.6	35.6
ANTPOF ALV	52.8					67.1	56
POSTPOF ALV (38)	59.8					81.6	71.3
VENT POF ALV	34.4	51.4		37.5		53.8	46.3
FC (36)	17.7	26.1		31.5		30.4	23.9
IOF-ALV							
CL					12.7	10.3	12.6
CW					8.1	6.6	8.4
M1W	58					34.6+	65.5
ANT POF	P3 MESO					P3 MESO	P4 PARA
POST POF	M2 POST					M2 PARA	M2 MESO
ORBIT	M3+					M3 META	M3 META
NASAL	P2 PARA					P2 MESO	P2 POST
CHOANAE	M2 MESO					M2 MESO	M1-M2
IOF	P4 MESO			P3 POST		P3 ANT	P3 POST
LACRIMAL						YES	NO
POSK (Depth)						YES (20.5)	YES (8.5)
ANT DEF*	1					1	0
VENT DEF*	2					2	1
AXIS POF	AV					HZ-AV	HZ
SUBNASAL	YES?					YES?	NO
AGE	Old	Old	?	Young	Adult	Adult	Young
SEX	?	?		?	Male	Male	Male
SUB-LOC.	Paris	Zad Baschi	Ketschawa	Kara Kend	Kopran II	Kopran	Kara Kend
TAXON	Mold.	Prost?	?	Mold.	?	Gettyi	Prost.
				40.8 (12)		250 (ANT)	39.5 (12)

Appendix 1 (continued)

SPECIMENS	W 86601 RLB 8402	A 4861	W 86600	W 86526	W 86527	W 86524	W 86516
I3-P2							
NN-P2							
NN-IOF							
NN-POF (31)							
NN-ORBIT							
P2/HEIGHT (25)						@95	
PROST-NSL (30)						@146	
APL/POF (33)	59.5						
DVH/POF (35)	35.5						
IOF-POF (34)	64	57					
POB (32)	24.1	43	28.8				
ORB/D (28)							
P2-ORBIT	145.6	158	140.5				
SNOUT/L (1)							
PALATE/L (2)	@95	107					
VOMER L (3)							
BASCR L (4)							
MUZZLE/W							@44.4
ANTPOF ALV	50						
POSTPOF ALV (38)	60.6		56.1				
VENT POF ALV	35	66.6	36				
FC (36)	18	44.5	22.4		41+		
IOF-ALV							
CL							13.2
CW							9.7
M1W							
ANT POF	P4 MESO						
POST POF	M3 MESO	M2 MESO	M2 POST				
ORBIT	M3+	M3 META	M3 META				
NASAL						P2 ANT	
CHOANAE	M2	M1-M2	M2				
IOF	P4 PARA	P4 MESO	P4 PARA	P3-P4			
LACRIMAL	YES		YES?				
POSK (Depth)	YES (8.0)		YES				
ANT DEF*	1		?				
VENT DEF*	1	1	1				
AXIS POF	AV	?	AV				
SUBNASAL	?	NO	?				
AGE	Old	Adult	Adult	Old	Young	?	Old
SEX	?	?	?	?	?	Female?	Male
SUB-LOC.	Ketschawa	?	Ketschawa	Ketschawa	Ketschawa	Ketschawa	Zad Baschi
TAXON	Mold. 33.5 (12)	Prost. 41 (12)	Mold?	?	?	?	?

Appendix 1 (continued)

SPECIMENS	W 8624	W 8623	RLB 8404	W 86511	W 86512	MMTT 13/1342
I3-P2	@78					75.2
NN-P2						76.4
NN-IOF						53.2
NN-POF (31)						85.3
NN-ORBIT						117.9
P2/HEIGHT (25)						90.8
PROST-NSL (30)						146
APL/POF (33)						61.7
DVH/POF (35)						34
IOF-POF (34)						43.9
POB (32)						33.3
ORB/D (28)		56.4				49.6
P2-ORBIT						152.7
SNOUT/L (1)	@99					104.8
PALATE/L (2)						110.5
VOMER L (3)						@98
BASCR L (4)						
MUZZLE/W	36.7					29.6
ANTPOF ALV						65
POSTPOF ALV (38)						89.7
VENT POF ALV			32.5	34.9	37	56.6
FC (36)			15.8	17.5	24.8	34.6
IOF-ALV						
CL	5.5					5.2
CW	4.4					3.1
M1W						49.8
ANT POF						P3-P4
POST POF						M2 PARA
ORBIT						M3 ANT
NASAL						P2 MESO
CHOANAE				DP4-M1		M1-M2
IOF				DP3PARA		P4 PARA
LACRIMAL						
POSK (Depth)						NO
ANT DEF*						0
VENT DEF*						0
AXIS POF						HZ-AV
SUBNASAL						NO
AGE	Adult	Old	Juvenile	Juvenile	Juvenile	Young
SEX	Female	?	?	?	?	Female
SUB-LOC.	Dschingirdera	?	Ketschawa	Ildtschi?	Ildtschi	UC 13 (-18)
TAXON	?	?	?	?	?	Urmiense
		37 (12)				131(18)
						303(23)
						27.2(12)

Appendix 2 Measurements of Upper Cheek Teeth.

SPECIMEN	KUAC 95090	KUAC 95086	KUAC 95334	KUAC 95333	KUAC 95040	KUAC 95331	KUAC 95089	KUAC 95330	KUAC 95329	MAR 359/1475	MAR 1474
P2APL	29.6	31.5	34.7	32	34.7	31.4	32.1		28.4	29.1	26.6
P2TRNW	24.6	21.2	20.6	23.4	25.4	22.4	24.4		22	21.5	21.2
P2PRTL	8	6.2	6.7	6.7	8	6.9	7.5		6.6	7.4	9.9
P2PRTW	6	4.3	4	4.6	5.1	4.8	4.5		4.7	4.2	6.3
P3APL	23.2	25.1	26.9	24.7	26.9	24.2	26.5	22.3	21.9	24.9	23.2
P3TRNW	25.6	23.4	21.4	24.4	26.9	24.2	26.1	23.5	21.9	24	23
P3PRTL	8	7.6	5.7	6.8	9	7.4	8.3	6.2	7.4	8.3	7.6
P3PRTW	5.7	4.8	3.5	4.1	4.6	4.8	4.5	4.3	5.4	4.3	4.9
P4APL	22.2	24.6	24.7	22.7	25.4	24.2	24.9	21.4	20.4	23.9	21.4
P4TRNW	25.4	21.6	20.2	24.3	25.7	24	24.5	21.9	22.1	24	22.6
P4PRTL	7.3	7.7		6.4	9.4	7	8.6	6.2	7.5	8.3	7.1
P4PRTW	5.2	4.4		4.2	4.4	4.7	4.6	4.2	5.2	4	4.6
M1APL	20.8	23.1		22.2	23.7	22.6	23	19.9	17.9	21.8	19.8
M1TRNW	23.7	21.3		22.4	23	22.1	24.1	21.5	21.2	22.7	23.7
M1PRTL	7.4	7.1		6.7	7.7	6.3	8.2	6.7	7.5	8.4	7
M1PRTW	4.3	4		4.1	4.3	4.3	4.4	4.2	5.1	3.7	4.8
M2APL	22	23.3		21.8	23.6	21.1	23	20.1	19.5	22.1	19.9
M2TRNW	21.9	19.9		20.8	22.7	21.7	22.3	19.2	20.3	22.6	22
M2PRTL	6.2	7		6.2	7.4	6.5	7.4	7.5	7.1	7.5	6.4
M2PRTW	4	3.7		3.6	3.9	4.6	3.8	3.8	5.1	3.9	4.2
M3APL	21.8	18.3		20.9	22.3	24.3	17.8	18	21	21.8	22.3
M3TRNW	20	13		16.4	18.1	16.2	14.5		18	19	20
M3PRTL	7	6.4		6.5	7.7	5.9	7	6.7	7	7.5	8.9
M3PRTW	3.7	2.7		3.4	3.4	3.2	3.5	2.7	4	3.4	4.3
P2-P4	75.3	81.4	87.7	79.6	87	79	82.9		70.1	78	70.5
M1-M3	65	64.4		64.8	68.9	65.2	62.9	57.9	57.7	65.9	63.3
P2-P3	142.1	145.7		143.3	155	143.5	146.7		128.5	143.4	133.1
PCB	1-1-1-1-2-1	1-1-1-1-1-1	1-1-?-?-?-?	2-4-4-3-2-2	2-1-2-1-1-1	1-1-1-1-2-1	1-1-2-2-1-1	?-1-1-1-1-1	2-1-1-1-1-1	2-2-2-3-1-2	0-1-1-1-1-1
PCL	12	16	15 (P3)	19	16	15	17	14	12	12	6
CL	9.8						0			11.2	10.6
CW	8.1						0			8.3	8.7
AGE	Adult	Young	very Young	Adult	Old	Young	Young	Adult	Old	Adult	Old
SEX	Male						Female			Male	Male
SUB-LOC.	Kyoto	Kyoto	Kyoto	Kyoto	Kyoto	Kyoto	Kyoto	Kyoto	Kyoto	Paris	Paris
TAXA	Prost.	?	Prost.	Prost.	?	Prost.	?	Mold.	Mold.	Prost.	Prost.

Appendix 2 (continued)

SPECIMEN	MAR 465	MAR 62	MAR 1477	MAR 71	MAR 1476	MAR 466	MAR 469	RLB 8003	MAR 66 1800	MAR 1799	MAR 1804	W 86601
P2APL	26.8	26.7		31.1		28.4	30.9	28.6	30.8	27.1	29	27.4
P2TRNW	22.4	20.8		22.5		22.9	23.6	21.4	21.8	20.2	22.3	21.3
P2PRTL	10.2	5.6		7.6		6.6	7.3	7.7	5.6	7.1	6.9	7.4
P2PRTW	6.8	4.2		4.8		5	4.3	5.1	4.5	4.9	4.8	4.2
P3APL	20.2	21.9	25.9	24.5	21	22.4	25.3	21	23.5	21	23.4	21.4
P3TRNW	22.9	21.5	26.7	24.6	22.3	24.3	25.5	23	22.1	21.8	24.4	22.9
P3PRTL	7.8	5.7	7.4	7.1	7.9	7	7.8	7.7	5.8	7.8	8	6.5
P3PRTW	5.8	4.2	4.6	4.9	5	5	4.2	5.6	3.7	4.7	4.8	4.4
P4APL	18.7	20	23.3	24.4	20.4	21.6	23.1	20.2	21.5	20	23.8	19.8
P4TRNW	22	20.8	24.9	23.9	22.6	24.4	24.4	22.7	22	21.9	24.1	22.2
P4PRTL	8.4	5.4	7.6	7.8	7.1	7	8	8.1	6.5	7.9	7.4	7.2
P4PRTW	5.3	3.9	4.4	4.4	4.4	4.7	4.1	5.8	4.2	4.8	4.4	4.6
M1APL	16.8	17.9	22	22.4	18.2	19.9	21	17.7	19.2	17.4	21.3	18
M1TRNW	23.2	19.8	23.2	23.4	21.4	22.1	22.4	21.5	19.8	20.3	23.6	21.2
M1PRTL	9+	5.6	7.2	7.8	6.8	6.9	8	8	6.5	7.6	8	7.3
M1PRTW	6	4	4	3.8	4.9	4.9	4.5	6.2	4.3	4.4	4.4	4.6
M2APL	17.9	19.7	22.4	22.8	20.4	20.5	21.8	18.9	19.2	18.9	21.2	19.4
M2TRNW	21.2	18.5	22.3	22.6	20.3	20.5	22.4	20.7	'19.6	19.3	21.5	19.6
M2PRTL	7.5	5.4	7.4	7.1	7.2	6.8	7.8	7.6	5.7	7.3	7.9	7
M2PRTW	4.9	3.9	4.2	4.3	4.5	4.2	3.4	5.2	4.3	4.7	3.4	4.4
M3APL	19.3	19.2	22.6	21.2	19.8	20.1	21.9	18.3				20.5
M3TRNW	20.4	16.1	29.3	17.2	18.7	18.5	19.7	18.8				18.4
M3PRTL	8.8	5.6	7.6	7	6.5	5.9	8.5	6.6				6.4
M3PRTW	6.3	3	3.6	4	3.5	3.8	3.8	4				3.6
P2-P4	65.9	69.6		79.3		71.5	79.6	69.6	73.6	67	76	67.7
M1-M3	54.1	57.3	67.3	66.2	58.6	60.7	64.8	55.6				58.1
P2-P3	120.4	127		145.4		132.7	144.5	125.3				125.9
PCB	0-1-1-0-1-1	1-1-1-1-0-1	?-2-2-1-3-2	1-2-1-3-1-1	?-2-2-1-1-1	2-2-3-1-1-1	1-2-2-1-1-2	1-2-3-0-1-1	1-1-1-1-1-?	0-2-2-2-1-?	1-1-1-2-1-?	1-1-1-0-1-2
PCL	0	13	21	16	13	14	15	13	12	13	13	1
CL									11.3			
CW									7.1			
AGE	Old	Adult	Adult	Adult	Adult	Adult	Adult	Old	Adult	Old	Old	Old
SEX												
SUB-LOC.	Paris	Paris	Paris	Paris	Paris	Paris	Paris	Paris	Paris	Paris	Paris	Ketschawa
TAXA	Prost.	Mold.	Mold.	Prost.	Mold.	Mold.	Mold.	Mold.	Mold?	?	?	?

Appendix 2 (continued)

SPECIMEN	MMTT 13/1342	A 4844	A 4861	W 86600	A 4847	W 86526	W 86527	W 86515	W 86504	W 86505	W 8659	W 8658
P2APL	34.2	34.1	33.7	28	33.1	34.2		31.4				35
P2TRNW	22	24.8	23.3	21.8	23.2	23.3		22.7				24.6
P2PRTL	6.9	7.7	6.6	5.8	6.6	8.2		6.4				8.4
P2PRTW	3.9	4	4.1	4.3	3.8	5.2		4				3.7
P3APL	26.2	27.7	26	22	25.7	25.2					23.4	27.5
P3TRNW	23.9	25.8	25.6	23	24.7	26.1				25.8	25.5	27.2
P3PRTL	6.2	8	6.4	5.9	6	8.1				8	7	8.6
P3PRTW	4.2	4	4.8	4.3	4	5.5				6.1	5.4	5
P4APL	26.1	24.6	25.1	20.8	23.6		26.2		20.3	23	22.3	26.3
P4TRNW	23.8	24.4	25.8	22.5	20.9		21.3		23.3	26.2	24.5	27.4
P4PRTL	6.2	7.8	6.4	6.2	6		6.7		7.9	8.6	8.5	9.4
P4PRTW	4.2	4.1	4.7	4.3	3		3.6		5.5	5.7	4.9	5.2
M1APL	22.5	22.8	23.2	19.3	23.3		24.9		18	18.5	18.8	
M1TRNW	22.2	22.8	23.4	20.4	21.6		21.3		23.2	25.1	22.8	
M1PRTL	6.3	7.3	5.9	6.4	5.5		5.8		8		7.9	
M1PRTW	4	3.8	4.3	4.1	3.7		3.6		6.2		5.2	
M2APL	22.6	23.6	22	19.9	22.8				18.9	19.7	20	
M2TRNW	21.5	20.4	22	19.3	20.2				21.4	24.2	21.4	
M2PRTL	6.1	6.8	5.8	6.4	6.4				7	7	8.3	
M2PRTW	4.1	3.6	4.4	4	3.4				5.6	6.5	3.8	
M3APL	19.5	17.2	21.6	18.8					22.9	22	21.9	
M3TRNW	15.5	14	19	17	15.5				18.8	21	19.3	
M3PRTL	6.1		6.9	5.4					7.2	7.3	6	
M3PRTW			4.1	3.6					4.5	4.6	4	
P2-P4	86.8	86.9	84.3	70.3	83.3							88
M1-M3	60.7	66.6	66.7	59	66.2				59.1	61.6	61.3	
P2-P3	148.2	152.1	151.2	129.7	149			143.2				
PCB	1-1-1-1-1-?	2-2-2-2-1-?	1-1-2-1-1-1	2-2-2-1-1-1	2-1-?-1-1-?	1-1-?-?-?-?	?-?-0-1-?-?		?-?-0-0-0-0	?-0-1-0-0-1	?-2-2-1-1-1	1-2-3-?-?-?
PCL	10+	16	9	10+	15+		14		0		11+	15(P4)
CL	5.2				12.6							
CW	3.1				8.4							
AGE	Young	Young	Adult	Adult	Young	Old	Young	Adult	Old	Old	Adult	Adult
SEX	Female				Male							
SUB-LOC.	UC 13(-18)	Kara Kend	?	Ketschawa	Kara Kend	Ketschawa	Ketschawa	Ketschawa	Kopran	Kopran	Kopran	?
TAXA	Urmiense	Mold.	Prost.	Mold?	Prost.	?	Prost?	?	?	?	?	Large size
											43.2 (12)	

Appendix 2 (continued)

SPECIMEN	A 4848	W 8623	W 8619	RLB 8401	A 4853	W 8613	W 8614	A 4850
P2APL	29.6		26.4	29.7	28.1	29.9	33.4	31.4
P2TRNW	22.2		21.6	22	22.8	21.3	24.3	22.7
P2PRTL	8		6.8	6.8	'6.2	6.8	6.5	6.5
P2PRTW	6.3		4.8	4.2	4	4.2	4.6	4.8
P3APL	22.5		21.8	23.1	23.5	22.6	25.3	24
P3TRNW	25.6		24	24.2	23.6	21.1	25.7	24.8
P3PRTL	8.8		7.7	7.7	6.2	7.2	7.4	6
P3PRTW	7		4.9	4.5	3.7	3.7	4.7	4.9
P4APL	22.4		21.2	21.4	22.7	20.6	24	23.8
P4TRNW	26.9		23.9	23.2	21.4	19.4	24.8	24.1
P4PRTL	9.2		8.2	7	6.7	6.7	7.5	7.3
P4PRTW	7.3		4.9	4.3	3.3	3.5	4.3	4.8
M1APL	19.9		18.9	20.8	21.9	20.5	22.6	21.3
M1TRNW	24.6		23.5	23.2	21	19.1	22.4	22.9
M1PRTL	8.3		8	7.5	5.9	7	7.4	7.2
M1PRTW	6.2		5	4.4	3.7	3.4	3.9	4.6
M2APL	19.9	20.7		20.3	21.4	18.7	22.9	21.6
M2TRNW	23.1	21.6		21.8	19.5	13.8	21.6	21.7
M2PRTL	8.4	7.4		7.2	6.1	6	6.8	6.1
M2PRTW	6.1	4.6		4.1	3.6	2.8	4.3	4.5
M3APL	21.4	20.5		19	16.9	20.3	19.8	20.2
M3TRNW	20.6	19.2		19.1	13.3		16.4	18.4
M3PRTL	7.4	7.5		6.9	6.2		7.5	6.2
M3PRTW	5.1	4.1		3.5	2.4		3.5	3.7
P2-P4	74.8		71.6	77.6	74.3	73.4	83	79.6
M1-M3	64			59.9	60.5	61.5	65.4	63.7
P2-P3	138			137.3	135.4	133.3	148.1	144.3
PCB	1-1-1-1-1-1	?-?-?-?-1-1	1-1-1-1-?-?	2-2-2-2-2-2	2-2-2-1-1-1	2-1-1-1-?-?	2-2-2-2-1-1	1-2-1-2-1-1
PCL	7	13(M2)	1	13	19+	8		17
CL				10.3				
CW				6.6				
AGE	Old	Adult	Old	Adult	Young	Young	Adult	Adult
SEX				Male				
SUB-LOC.	Zad Baschi	?	Ketschawa	Kopran	?	Kopran	Ketschawa	Ketschawa
TAXA	Prost.	?	Prost?	?	?	?	?	?
		37 (12)						

Appendix 3 Measurements of Lower Cheek Teeth.

SPECIMENS	O 15 (PARIS)	MAR 69	MAR 463	MAR 457	MAR 462	MAR 464	MAR 63	MAR 89
p2apl	26.3		27.7	29	24.6	27.9	27.5	25.5
p2amcw	10.6		11.4	10.2	10.8	10.4	10.6	10
p2petw	12.3		12.6	12	12.7	12.5	12.7	11.3
p2mcms	13.2		11.2	12.2	11	12.1	12.8	11.2
p3apl	23.7		25.4	25.9	22.2	24.9	24.1	23.1
p3amcw	13.5		13.8	13.5	14.3	14	14.1	13
p3petw	12.8		12.7	11.8	13.1	13.1	13.2	11.8
p3mcms	15.6		14.4	16.3	14.6	15.6	15.6	15.2
p4apl			24.4	25.5	22.3	24.9	24.6	23.1
p4amcw			13.5	13.4	14.6	13.6	13.6	13
p4petw			12.3	11.9	12.3	13.3	12.4	11.8
p4mcms			13.2	15.1	13.8	14.4	14.4	15.2
m1apl			22	23.1	19.8	23	23	23
m1amcw			12.1	12.1	12.8	12.4	12.2	13.4
m1petw			10.4	10.1	10.5	10.6	10.7	12.1
m1mcms			13	13.9	12.3	14.1	14.2	13.7
m2apl			22.8	22	20.9	23	22.7	20.8
m2amcw			11.5	11.7	11.8	12.2	12	12.3
m2petw			9.7	8.8	9.6	10.1	10.1	10.7
m2mcms			12.2	12.6	12.4	13.1	12.9	12.9
m3apl			24.1	24.6	24.9	24	24	20
m3amcw			9	10	10.3	10.3	10.2	12.2
m3petw			8.5	8.2	8.7	8.5	8.2	10.1
m3mcms			10.3	10.9	11.7	10.4	11.2	13.3
p2-m3			145	149.7	134.3	146.1	145.5	
p2-p4			77.4	79.7	69.8	76.5	76.2	71.5
m1-m3			68.4	70.9	65	70.4	70	
prtsd	0-0-?-?-?-?		0-1-1-1-0-0	0-?-1-1-1-?	0-1-?-1-?-0	0-1-1-1-0-0	0-1-1-1-?-?	0-1-1-1-?-?
CL	9.4	9.8		4.8				
CW	7.6	8.1		3.6				
i3-p2	73.8	81.8		65.3				
muzzle width	43.6	34.5		35.4				
p2h	42			47.3				
m1h				70.7				
double knots	HIPP	?	HIPP	HIPP	HIPP-C	HIPP	HIPP	?
AGE	Adult	Adult	Adult	Adult	Adult	Adult	Adult	Young
SEX	Male	Male	?	Female	?	?	?	?
SNOUT	YES	YES	NO	YES	NO	NO	NO	NO
SUB-LOC.	Paris	Paris	Paris	Paris	Paris	Paris	Paris	Paris

Appendix 3 (continued)

SPECIMENS	MAR 460	MAR 461	MAR 468	MAR 76	MAR 458	MAR 88(73)	MAR 73(88)	MAR 456
p2apl	26.1	26	27.4	23	27.9	30	30.2	29.1
p2amcw	10.5	10.7	10.7	12.6	9.2	9.8	9.5	11.5
p2petw	11.6	11.5	13	11.2	10.7	11.9	12	14.8
p2mcms	13	12.6	10.7	12.9	12	12	11.9	12
p3apl	22.5	23.4	25.1		23.8	26.8	27	25.5
p3amcw	12.8	13	13.9		12.3	12.9	12.2	15.9
p3petw	11.6	11.4	13.8		11	12.4	12.2	14.3
p3mcms	14.2	14.3	14.1		14.3	15	15.2	15.3
p4apl	22.3	22.4	23.7		23.5	27.4	26.5	24.7
p4amcw	12.6	12.4	13.1		12.3	11	11.3	15.2
p4petw	11	10.5	12.8		10.3	11.2	11.1	13
p4mcms	13.7	14	12.8		13.8	13.9	13.2	14.4
m1apl	20.8	21.4	22	21.8	20.9	23.8	24.2	21.2
m1amcw	11.7	12.1	11.5	11.7	11	10.5	10.6	13.6
m1petw	10.2	10.3	10.8	9.8	9.6	10	9.6	11.5
m1mcms	12.4	12.7	12.6	12.6	12.4	13.9	14.2	13.2
m2apl	21	21.2	22.7	21	20.7	24	23.7	22.6
m2amcw	10.9	10.8	11.2	10.3	9.5	10.2	10.3	13.2
m2petw	9.4	9.3	9.9	8.7	8.5	10.4	9.1	10.3
m2mcms	12.4	12.6	12.1	11.4	12.2	13.2	12.8	13.4
m3apl	23	22.4	22.5	22.8	22.2	23.5	23.7	28.4
m3amcw	9	9.3	8.9	9.3	7.9	8.6	8.5	11.4
m3petw	7.4	7.6	7.2	7.9	7.2	7.2	7.3	9
m3mcms	11	10.8	9.6	10.4	9.3	10.4	10.2	12.5
p2-m3	136.2	137.5	142.8		139.2	155	154	151.2
p2-p4	71	72.2	76.6		72.7	84	84.3	78.8
m1-m3	65.3	65.5	66.7	66.5	67.8	71	71.2	72.8
prtsd	0-?-?-1-0-0	0-?-?-1-0-0	0-0-0-1-?-0	?-?-0-0-0-0	0-1-1-1-0-0	0-0-0-1-0-0	0-0-0-1-0-0	0-1-1-1-1-?
CL					9.2			14
CW					8.1			11.1
i3-p2					58.3			85
muzzle width					@32			38.2
p2h	39	42.9	48.2		35.1			46.7
m1h	57.3	58	63.5					70.3
double knots	HIPP-C	HIPP	HIPP	HIPP	HIPP	CAB	CAB	HIPP
AGE	Adult	Adult	Adult	Adult	Adult	Young	Adult	Old
SEX	?	?	?	?	Male	?	?	Male
SNOUT	NO	NO	NO	NO	YES	NO	NO	YES
SUB-LOC.	Paris	Paris	Paris	Paris	Paris	Paris	Paris	Paris

Appendix 3 (continued)

SPECIMENS	MAR 456(R)	MAR 67	MAR NO	W 8616	W 8617	W 8618	W86523	W8:523(R)
p2apl	29.4	24.4	24.5					
p2amcw	12.3	9.7	10					
p2petw	15.3	11.2	10.5					
p2mcms	12.8	10.4	10.6					
p3apl	25.5	22.2						22.5
p3amcw	15.8	12						14
p3petw	14.3	11.6						14.2
p3mcms	15.2	13.4						
p4apl	24.5	23.2					22.6	22.7
p4amcw	15.8	12.7					14.5	14.6
p4petw	13	11.1					12.9	12.9
p4mcms	14.4	13.2					16.3	16.1
m1apl	22.2	18.9					20.6	20.5
m1amcw	14.3	11.2					13.8	13.8
m1petw		10					12	11.7
m1mcms	12.8	11.4					13.5	13.4
m2apl	23.3	19.3					22.3	22.5
m2amcw	13.6	10.7					12	12
m2petw	10.2	9.2					9.9	10
m2mcms	12.8	11.1					13.6	13.2
m3apl	28.5	23.5						
m3amcw	11.6	9.7						
m3petw	9.1	8.7						
m3mcms	12.4	10.4						
p2-m3	151.8	130						
p2-p4	79.4	69.7					@71	@69
m1-m3	72.8	60.5						
prtsd	0-1-1-1-1-?	0-1-1-1-1-?						
CL			9.7	8.5	10.2	10.8		
CW			8.2	7.1	9	7.7		
i3-p2			72.9					
muzzle width			35.4	47.3	@44	47.4		
p2h			40.6				51.1	
m1h								65.7
double knots	HIPP	HIPP	HIPP	?	?	?	?	?
AGE	Old	Adult	Adult	Adult	Adult	Adult	Old	Old
SEX	Male	?	Male	Male	Male	Male	?	?
SNOUT	YES	NO	YES				NO	NO
SUB-LOC.	Paris	Paris	Paris	Ketschawa	Ketschawa	Kara Kend	Ketschawa	Ketschawa

Appendix 3 (continued)

SPECIMENS	W86520	W86521	W86518	W86519	W86513	W86514	W86510	W86508(9)
p2apl	31.7		26		24.8		27.9	
p2amcw	11.3		10.4		9.8		10.5	
p2petw	13.5		12.7		12		12.9	
p2mcms	11.8		10.1		11.5		12.6	
p3apl			23.4					22.8
p3amcw			13.5					11.8
p3petw			12.4					11.9
p3mcms			14.2					14.2
p4apl		23.5	22.4	22.9			23.7	22.9
p4amcw		14	12.8	12.8			13.9	11.6
p4petw		11.6	11.2	11.2			12.4	10.8
p4mcms		14.8	13.7	14.1			14.8	13.8
m1apl		21.8	20.4	21			21.6	20.8
m1amcw		13.6	11.2	11			12.8	10.7
m1petw		11.3	9.5	9.7			11.2	9.6
m1mcms		12.7	12.4	12.9			13.2	12.3
m2apl		22.3		21			23.4	20.4
m2amcw		12.1		11			12	9.7
m2petw		10.1		9.7			10	8.2
m2mcms		13.1		14			13.5	11.3
m3apl				24.5				22.7
m3amcw				9.8				9
m3petw				8.4				7.3
m3mcms				10.8				9.8
p2-m3								
p2-p4			71.9				75.4	
m1-m3				66.3				63.8
prtsd		?-?-1-1-1	0-1-1-1-?-?	?-?-0-1-0-1			?-?-0-1-0-?	0-0-0-0-0-0
CL						11.3	11.2	
CW						11.2	9.1	
i3-p2						76.2		
muzzle width						38.4	@40	
p2h	45.8						44.7	58.2
m1h				54.1				
double knots	HIPP	HIPP	HIPP	HIPP	?	?	HIPP	HIPP
AGE	Young	Old	Adult	Adult	Old	very Old	Old	Adult
SEX	?	?	?	?	?	Male	Male	?
SNOUT	YES	NO	NO	NO	NO	YES	YES	NO
SUB-LOC.	Ketschawa	Ketschawa	Kopran	Kopran	Ketschawa	Ketschawa	Ildtschi	Ildtschi

Appendix 3 (continued)

SPECIMENS	W86509(8)	W86506	W86507	W86501	W86503	W-NO	W8622(R)	W8622(L)
p2apl					26	27.1	25.5	
p2amcw					10.4	10.1	11.3	
p2petw					11.7	12.4	14.4	
p2mcms					11.4	10.9	11.5	
p3apl	23.2			22.9	24.5	24.6	23.6	26.6
p3amcw	11.7			14.2	13.3	13.2	14.2	15.3
p3petw	12.1			13.6	13	12.7	12.7	12.8
p3mcms	14.2			15	14.2	15.6	15.1	18
p4apl	23.2	23.7		22.9	23.7	23.5	23.3	25.8
p4amcw	11.9	14.3		14.6	13.4	13.1	13.8	13.9
p4petw	11	13.6		12.8	11.8	11.8	12.1	12.8
p4mcms	13.8			15.2	13.4	14	14.5	17.4
m1apl	21	20.9		19.6			21.2	23.2
m1amcw	10.8	13.2		12.2			12.9	12.4
m1petw	9.5	11.8		11.7			11.1	10.4
m1mcms	12.6	12.6					13.4	14.5
m2apl	21.2	21					22.7	24
m2amcw	9.8	12.8					12.1	12.1
m2petw	7.8	10.3					10.4	
m2mcms	11.3	11.9					13.2	14.6
m3apl	23.1	29.6					27.8	27
m3amcw	8.9	11.7					11	10.5
m3petw	7.4	9.5					8.9	9.1
m3mcms	10.2	11.6					12.1	14.4
p2-m3							142.5	
p2-p4					74.9	75.8	71.7	
m1-m3	65.4	71.7					71.1	74.4
prtsd	0-0-0-0-0-0	0-?-0-1-1-1		0-1-1-1-?-?	0-0-0-?-?-?	0-1-1-?-?-?	0-1-1-1-1-0	0-?-1-?-?-1
CL								
CW								
i3-p2			69.8					
muzzle width			37.3					
p2h						37.5		54.1
m1h							65.6	72.7
double knots	HIPP	HIPP?	?	HIPP	HIPP	HIPP	HIPP	HIPP
AGE	Adult	Old	Young	Old	?	Adult	Old	?
SEX	?	?	Male	?	?	?	?	?
SNOUT	NO	NO	YES	NO	NO	YES	NO	NO
SUB-LOC.	Ildtschi	Ildtschi	Ildtschi	Kopran	Kopran	Kopran	Ketschawa	Ketschawa

Appendix 3 (continued)

SPECIMENS	A4851(R)	A4851(L)	W8621	RLB 8406	RLB 8407	RLB 8408	W8620	RLB 8405
p2apl	30.7							24.2
p2amcw	11.2							8.8
p2petw	14.4							10.6
p2mcms	10.3							9.4
p3apl	27.8	27.3	24.3					21.8
p3amcw	13.9	13.6	14					11.5
p3petw	13.6	13.4	13.2					11
p3mcms	15.8	15.8	15.5					12.9
p4apl	26.3	27.6	23.1	20.2				22.5
p4amcw	13	12.2	13.8	13.6				11.2
p4petw	10.4	11.3	11.8	10.7				10
p4mcms	13.7	13.9	14.2	13				12.2
m1apl	24.4	24.2	20.9	16.7	17.9	17.5		20.6
m1amcw	11.4	11.6	12.4	12	11.7	12.3		10.7
m1petw	10.1	9.8	10.6	9.8	11	11		9.2
m1mcms	14.7	15	12.6	10.2	11.6	12		11
m2apl	25.3	25.8	21.8	18.2	19.4	18.7		20.5
m2amcw	10.5	10.6	11.7	10.4	10.7	11		9.8
m2petw	8.9	9.2	9.4	8.5	8.8	9.4		8.7
m2mcms	12.9	14	12.4	10.4	11	11		10.1
m3apl								
m3amcw								
m3petw								
m3mcms								
p2-m3	153.5							
p2-p4	84							
m1-m3	69.7							
prtsd	0-?-?-?-?-?	1-1-1-1-1-?	1-1-1-1-1-?	?-?-1-1-1-?	?-?-?-0-0-?	?-?-?-0-0-?		0-0-0-0-0-?
CL							11	
CW							9.8	
i3-p2								
muzzle width							31.6	
p2h								
m1h		65	63.2					
double knots	HIPP?	HIPP?	HIPP	HIPP	HIPP	HIPP	?	HIPP
AGE	Young	Young	Adult	Old	Adult	Adult	Adult	Adult
SEX	?	?	?	?	?	?	Male	?
SNOUT	NO	NO	NO	NO	NO	NO	YES	NO
SUB-LOC.	Kopran	Kopran	Kopran	Kopran II	Kopran II	Kopran II	Kopran II	Kopran II

Appendix 3 (continued)

SPECIMENS	A4846(L)	A4846(R)	A4845(R)	A4845(L)	A4866(L)	W8612	A 4867	95324 KUAC
p2apl	24.2	23.2	31.5	30.4	29.5	29.3		
p2amcw	9.5	10.4	10.7	10.8	10.8	10.8		
p2petw	12.1	12.3	13.9	13.7	14.3	13.4		
p2mcms	7.5	7.6	12.4	12.3	15.4	11.1		
p3apl	23	22.1	28	27.8	27.7	25.4		
p3amcw	14.2	14	16	15.6	14.4	13.6		
p3petw	12.7	12.7	14.3	14.3	14.7	13.7		
p3mcms	13.9	14	17.9	17.7	18.3	14.6		
p4apl	22.1	21.9	26.5	26.3	27.8	26.7		
p4amcw	14	14	17	16.6	14	12.9		
p4petw	12	11.8	13	12.7	13.3	12.4		
p4mcms	13.1	13.1	18.1	17.8	17.4	13.4		
m1apl	21.2	20.7	25	24.8	25.6	23.1		
m1amcw	12.5	12.6	14.6	14.6	12.1	11.3		
m1petw	10.4	10.6	11.1	11.6	10.8	10.1		
m1mcms	12.2	12	15.5	15.8	15.6	13.3		
m2apl	21.2	21.8	24.4		27.4	23.8		22.8
m2amcw	12.3	12.4	13.4		10.9	10.4		12.3
m2petw	9.7	9.8	10.7		8.7	9		10.1
m2mcms	12	12.4	14.8		14.8	13.3		13.2
m3apl	26	26	29.3		25.3	24.6		25.9
m3amcw	10.8	11.1	12			9.7		11.5
m3petw	9	9.1	9.9			8		9.7
m3mcms	11.1	11	13.6			10.8		11.5
p2-m3	137.9	135.4	163.5			150.1		
p2-p4	69	67.6	85.5			80.1		
m1-m3	68.5	68.1	78.5			71.3		
prtsd	0-1-1-1-1-0	0-1-1-1-1-0	0-1-1-1-1-1	0-1-1-1-?-?	0-1-1-1-1-?	0-?-?-1-?-?		?-?-?-?-1-0
CL	5				6.3		9.4	
CW	4.1				5.5		8.5	
i3-p2	82.5				77.7			
muzzle width	52.3				32.4		40.6	
p2h	46.6				47.9	48		
m1h					70	65.3		
double knots	HIPP	HIPP	HIPP	HIPP	HIPP	HIPP	?	HIPP
AGE	Adult	Adult	Adult	Adult	Young	Young	Adult	Adult
SEX	Male	Male	?	?	F	?	Male	?
SNOUT	YES	YES	NO	NO	YES	NO	YES	NO
SUB-LOC.	Kopran	Kopran	Zad Baschi	Zad Baschi	Kopran	Ketschawa	Ketschawa	Kyoto

Appendix 3 (continued)

SPECIMENS	95077 KUAC	95078 KUAC	95036 KUAC	95039 KUAC	95034 KUAC	95026 KUAC	95035 KUAC	95337 KUAC
p2apl	25.9		25.8	27.3	31.5		29.5	27.6
p2amcw	9.6		9.8	11.1	10.6		11.1	11.4
p2petw	11.1		11.3	13.8	12.3		12.8	12.9
p2mcms	10.4		10.6	12.2	11.6		11.2	12.3
p3apl	23.4	21	23.6	24.4	26.6		25.9	24.4
p3amcw	12.3	13.4	12.9	14.1	11.9		13.8	14.5
p3petw	11.5	13.2	11.9	13	11.7		13.2	13.2
p3mcms	13.6	14	14.1	15.4	12.9		14.3	15.6
p4apl	23.5	21.3	23.8	24.4	24.7		24.9	24.5
p4amcw	10.5	14.5	13.3	13.3	9.5		13.6	15
p4petw	9.8	12.5	10.8	11.9	9		11.7	13
p4mcms	12.1	13.6	13.5	14.2	10.8		14	15.1
m1apl	22.3	19.2	22.2	23.5	29.3	23	23.4	21.3
m1amcw	10.9	12.9	11.6	12.6	11.3	12.9	12.8	12.76
m1petw	9.3	11.2	10	9.8	9.4	10.7	10.9	11
m1mcms	13.1	11.6	12.8	14.5	14.3	13.5	13.8	12.6
m2apl	23.2	20	23.3	23.4	25.8	23.9		
m2amcw	9.1	11.7	10.8	11	9.2	12.1		
m2petw	8.5	9.4	8.3	9.6	8.1	10.3		
m2mcms	12.1	11.3	11.8	13.1	11.4	13		
m3apl	14.7	25.2		23		25		
m3amcw	6	10.3		9.1		11		
m3petw		8.7		8		8.5		
m3mcms	8	11.2		10.5		11		
p2-m3	131.6	129.5		146.1				
p2-p4	72.7	64	73.2	76.2	84.5		79.8	76.1
m1-m3	58.7	63.9		69.7		71.9		
prtsd	0-0-0-0-0-0	0-1-1-1-1-1	0-0-0-0-0-?	0-1-0-1-0-0	0-0-0-0-0-?	?-?-?-0-0-0	0-0-0-1-?-?	0-1-1-1-?-?
CL		4.6	9.7					
CW		4.5	9.3					
i3-p2		73.8	68.3					
muzzle width		31.8	35.8					
p2h		37.6	40.6	46			52	@48
m1h			57	67.4			63.4	71.3
double knots	CAB	HIPP	HIPP	HIPP	?	HIPP	HIPP	HIPP
AGE	Young	Old	Adult	Adult	very Young	Adult	Adult	Adult
SEX	?	Female	Male	?	?	?	?	?
SNOUT	NO	YES	YES	YES	NO	NO	NO	NO
SUB-LOC.	Kyoto	Kyoto	Kyoto	Kyoto	Kyoto	Kyoto	Kyoto	Kyoto

Appendix 4 Measurements of Deciduous Upper Cheek Teeth.

SPECIMEN	MAR 1797	MAR 1796	MAR 65	MAR 1798	MAR 1795	W 86512	W 86511	RLB 8404	KUAC 95335	KUAC 95332	KUAC 95046	KUAC 95045	KUAC 95336
P1APL	4.9	8	9.8		12.4							13.3	
P1TRNW	5.7	4.7	4.7		8							9.7	
DP2APL	34.6	34.4	36.2	29.8(P2)	30	36.6	35.9	31.8	30.5	34	36.7	36.7	36.1
DP2TRNW	22		23.3	20.1(P2)	20.1	21	20.8	21.4	17.9	22.1	22.3	22.9	17.9
DP2PRTL	5.3	8.2	6.4	7.8(P2)	6.3	6.2	6.1	6	5.8	6.8	6	6.5	6.4
DP2PRTW	4.2	6	5	3.6(P2)	4	4.6	4.2	4.9	3.6	5.2	4.5	5.5	3.3
DP3APL	25.2	26.3	27	23.7(P3)	25.5	26.2	26	23.9	23.7	25.9	26.5	27	28.3
DP3TRNW	21.6	22.1	23.4	20.5(P3)	20.4	22.2	21	21.9	18.7	22.7	20.5	23.1	17.7
DP3PRTL	5.7	6.8	7	9.2(P3)	6.1	5.5	6.3	6.1	5.3	6.6	5	6.4	6
DP3PRTW	4.8	5.1	5.9	3.2(P3)	3.7	5.2	4.8	4.8	3.6	5.3	4.5	6	2.9
DP4APL		27.2	29.7	23.7	26.4	27.3	27.7	25.8	24.7	26.9	28.7	26.8	
DP4TRNW		21.1	22	22.7	17.4	20	19.5	19.8	16.5	21.8	18.3	21.6	
DP4PRTL		7.4	6.5	7.4	6.1	5.7	6.7	7.4	5.7	7.2	5.9	6.9	
DP4PRTW		4.6	5	5.6	2.7	3.9	3.8	4	3	4.8	3.5	5.3	
M1APL		23.9	25.3	22.5				21.7		23.9		25.1	
M1TRNW		18.9	19.5	21.7				16.3		19.7		20.1	
M1PRTL		7	6.2	6.8				5.1		7.8		7.4	
M1PRTW		3.9	3.4	3.3				2.3		3.1		4	
M2APL				21.5				21.1					
M2TRNW				18				17.5					
M2PRTL				6.8									
M2PRTW				2.9									
DP2-DP4		88.4	92.8	78	82.8	93.6	91	81.9	79.3	86.4	93.8	90.9	
PCL		16(DP4)	17(DP4)	17+	8 (DP4)	7(DP4)	12(DP4)		9+(DP4)	17(DP4)	10(DP4)	19(DP4)	
CL													
CW													
SEX	?	?	?	?	?	?	?	?	?	?	?	?	?
SUB-LOC.	Paris	Paris	Paris	Paris	Paris	Ildtschi	Ildtschi	Ketschawa	Kyoto	Kyoto	Kyoto	Kyoto	Kyoto
TAXA	Mold?	Prost?	Mold.	?	?	Mold?	Mold.	Mold.	Mold.	Prost.	Prost.	Prost?	Mold.
REMARKS				PALATE L= 99.7									

Plate 1

1. Lateral view of a skull of *H. gettyi* (KNHM RLB 8401). Female.
2. Lateral view of a skull of *H. urmiense* (MMTT 13/1342). Female.
3. Lateral view of a skull of *H. prostylum* (KUAC 95090). Male.
4. Lateral view of a skull of *H. prostylum* (KUAC 95089). Female.

Solid bar is 10 cm.

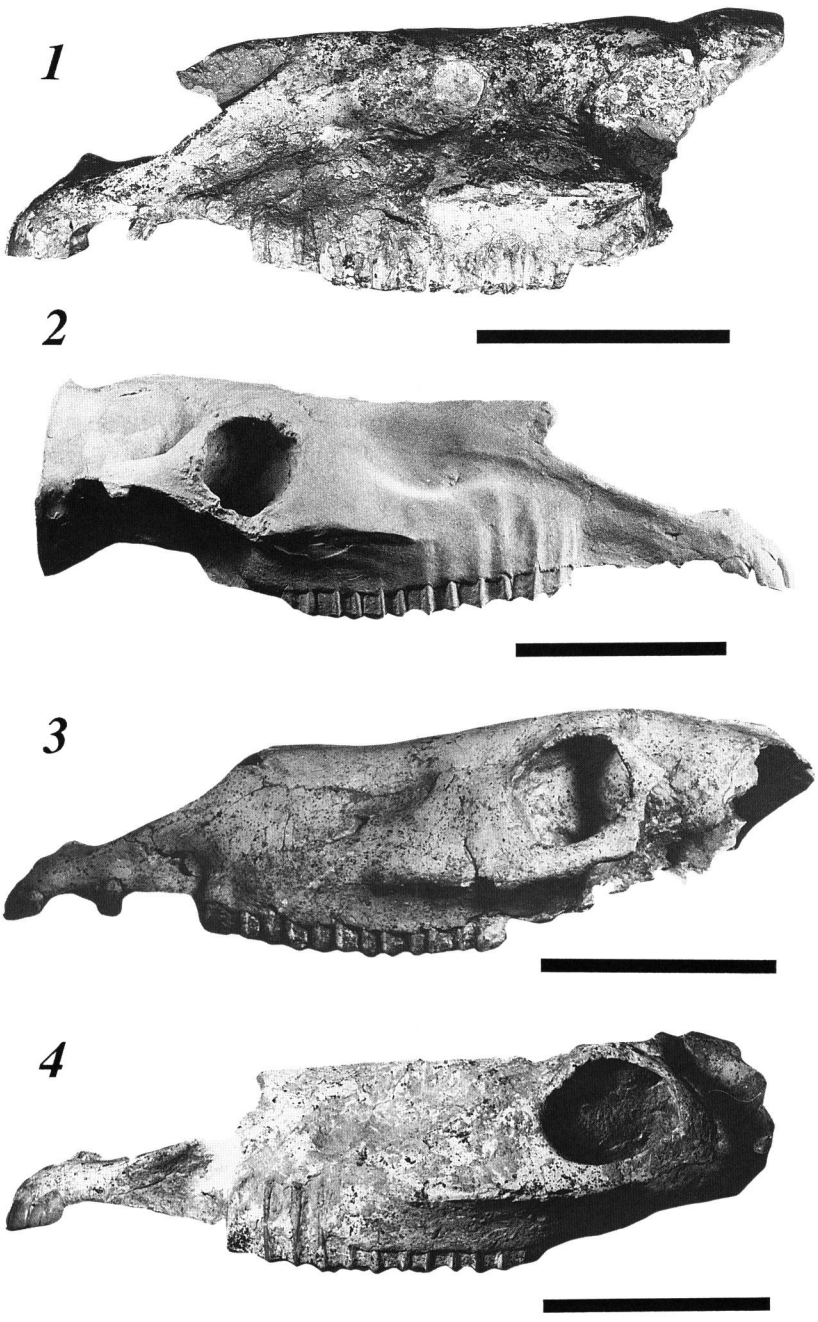
1
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Plate 2

1. Ventral view of skull of *H. gettyi* (KNHM RLB 8401).
2. Ventral view of skull of *H. urmiense* (MMTT 13/1342).
3. Ventral view of skull of Skull of *H. prostylum* (KUAC 95089).
4. Ventral view of a maxilla with upper snout region (MNHM 66-1800) with rounded arrangement of incisors (I1-I3). Male. This might be assigned to *H. moldavicum*.

Solid bar is 10 cm.

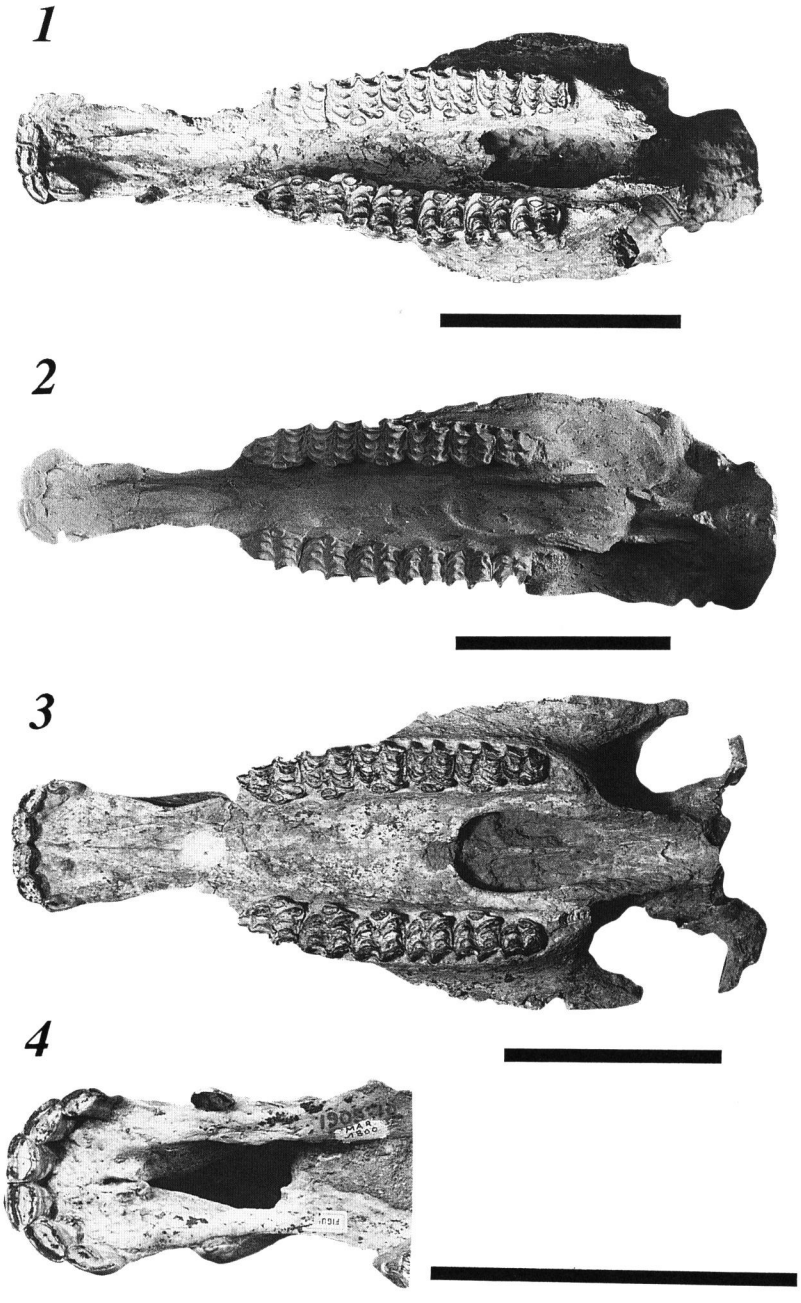
1
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Plate 3

1. Lateral view of a skull of *H. moldavicum* (KUAC 95329).
2. Lateral view of a skull of *H. moldavicum* (KUAC 95330).
3. Lateral view of a skull of juvenile of *H. prostylum* (KUAC 95046) with DP2-DP4.

Solid bar is 10 cm.

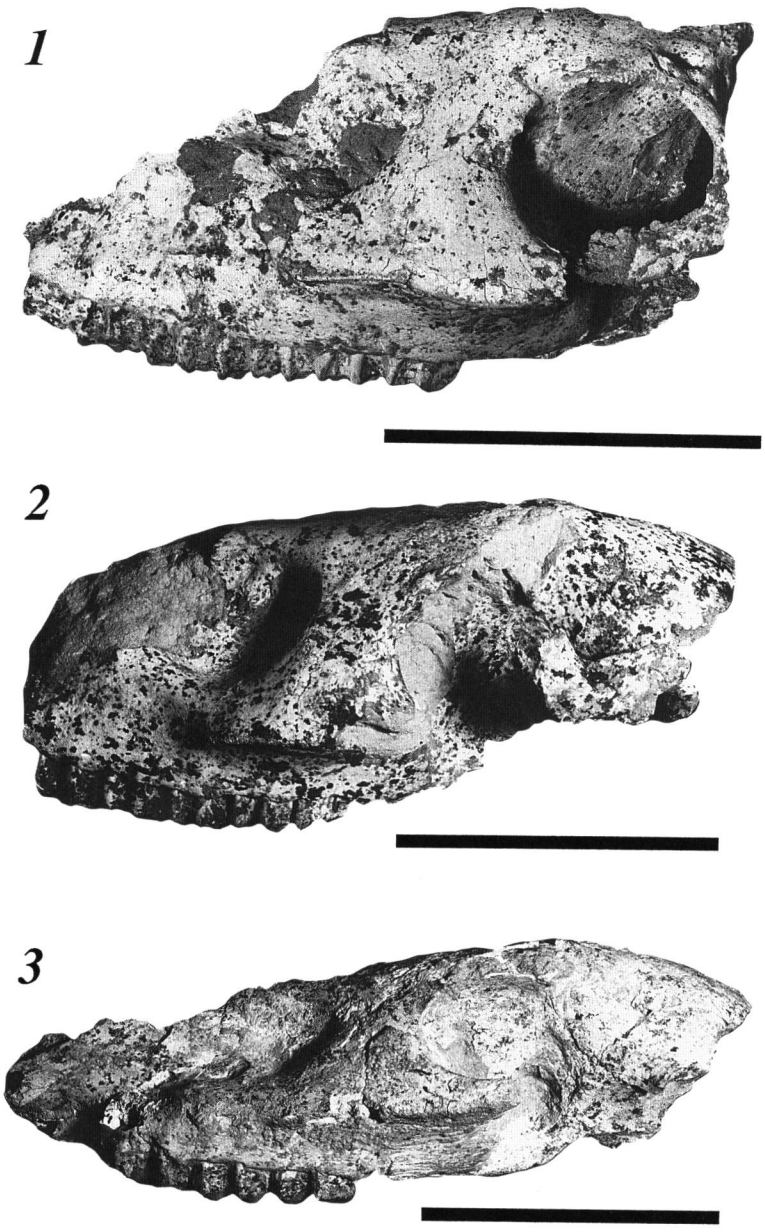
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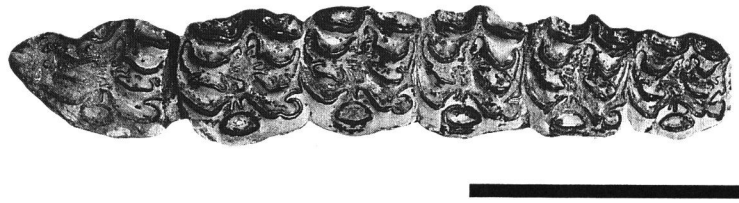
Plate 4

1. Occlusal morphology of left cheek teeth row of *H. gettyi* (KNHM RLB 8401).
2. Occlusal morphology of left cheek teeth row of *H. urmiense* (MMTT 13/1342). Plaster model.
3. Occlusal morphology of left cheek teeth row of *H. prostylum* (KUAC 95089).
4. Occlusal morphology of left cheek teeth row of *H. moldavicum* KUAC 95329).
5. Occlusal morphology of right lower cheek teeth row with large size (KNHM A 4845) from the sub-locality Zad Baschi, probably of *H. prostylum*. The hipparionid type of the doubl knots.

Solid bar is 5 cm.

1



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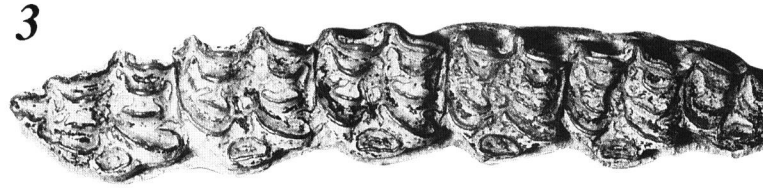
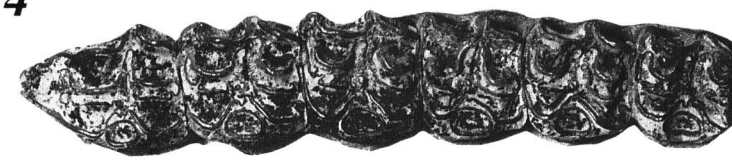
3



4



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